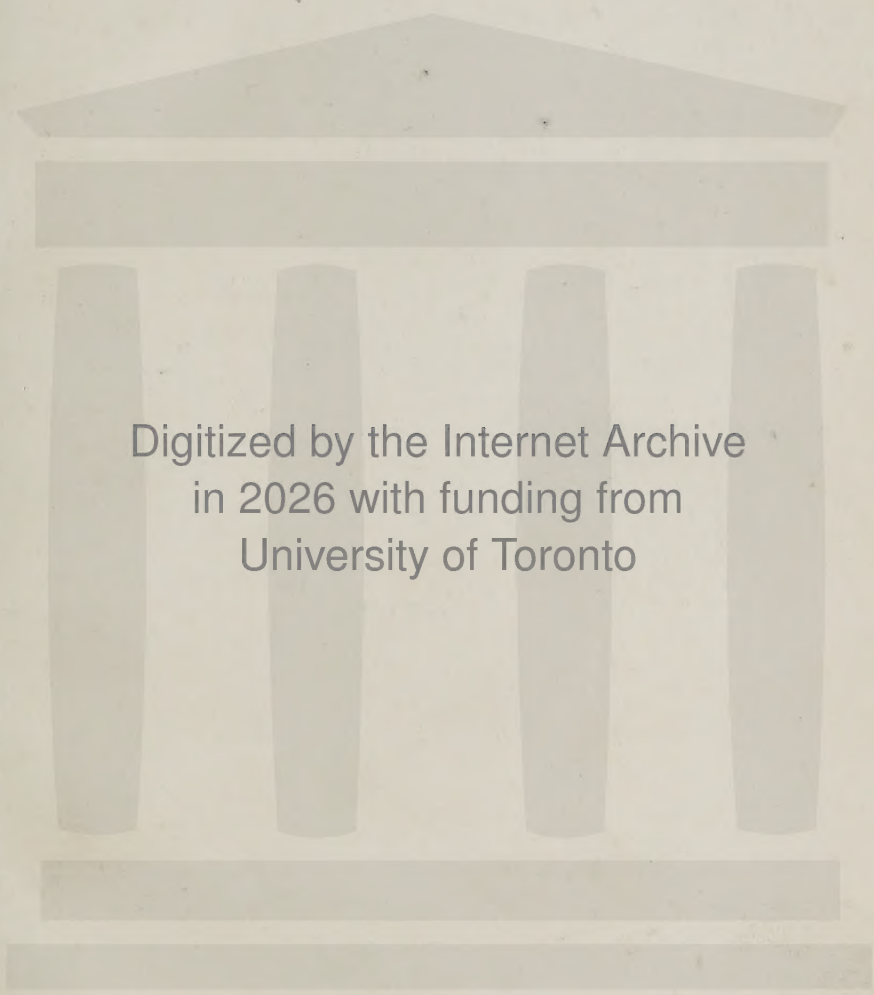
PRINCIPLES OF ANIMAL BIOLOGY

HOGBEN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PRINCIPLES OF ANIMAL BIOLOGY

BY THE SAME AUTHOR

THE PIGMENTARY EFFECTOR SYSTEM (*Oliver & Boyd*)

COMPARATIVE PHYSIOLOGY (*Sidgwick & Jackson*)

THE COMPARATIVE PHYSIOLOGY OF INTERNAL SECRETION (*Cambridge University Press*)

INTRODUCTION TO RECENT ADVANCES IN COMPARATIVE PHYSIOLOGY (*Collins*)

TWO EXTREMES OF COLOUR CHANGE IN THE COMMON FROG

Showing the influence of pituitary hormone on colour-change in frogs. *Left*—Control specimen, in dry light surroundings. *Right*—Specimen kept in the same surroundings, but injected with extract of ox-pituitary (posterior lobe). (*See* Chapter V.)

Biol

PRINCIPLES OF ANIMAL BIOLOGY

BY

LANCELOT T. HOGBEN

M.A. (CANTAB), D.SC. (LOND.)

PROFESSOR OF SOCIAL BIOLOGY IN THE UNIVERSITY OF LONDON; FORMERLY PROFESSOR OF ZOOLOGY IN THE UNIVERSITY OF CAPE TOWN; ASSISTANT PROFESSOR OF ZOOLOGY, MCGILL UNIVERSITY AND LECTURER IN EXPERIMENTAL PHYSIOLOGY, EDINBURGH UNIVERSITY

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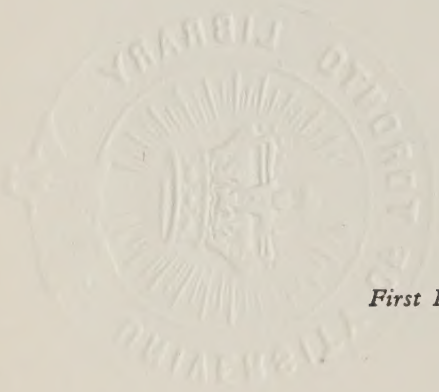

First Published in 1930

Printed in Great Britain

TO

H. G. WELLS

FOREWORD

INCREASING recognition of the cultural value of biological study carries with it both dangers and opportunities. The chief danger is lest the discipline of older and more exact sciences like chemistry and physics may be sacrificed to make place for miscellanies of easily memorisable facts illustrating nothing which can be properly regarded as scientific generalisations. Biological works are still replete with statements referred to as "laws," whereas they are in reality mnemonics. Because of the complexity of its subject-matter, biological study necessitates the apprehension of a great diversity of data, which have been collected and classified by laborious effort. It may happen in the early growth of any branch of knowledge that those on whom this task falls in time forget the wood for the trees or are even attracted to studying the subject because their preference for trees is greater than their interest in the wood itself. Hence zoological text books in the past have been largely filled with tedious descriptions of the architecture of the body based on dissection of dead specimens. They thus leave in the mind of the reader the impression that zoology is concerned with corpses rather than with animals, as the word implies. If zoology is handled as a cultural subject by those who are interested in its subject-matter in the same way as one is interested in stamp collecting, its cultural value will not be considerable. If it is taught by those who regard it as the experimental study of the properties of living matter, biology will not provide an *easy* substitute for physics and chemistry. On the contrary, it is well suited to stimulate an interest in

these subjects, where such an interest does not previously exist.

An author who is rash enough to add to the number of existing text books might be expected to offer some explanation of the special features of his own contribution. A somewhat different plan is usually adopted in English and American manuals. Most English text books for first-year students of zoology in the University and higher forms of schools are based on the "type system" introduced by Thomas Henry Huxley. They tend to be packed almost exclusively with the same type of facts as the student encounters in his practical work and can find in his laboratory manual. It has been the tradition in British, though not in American, text books to describe the anatomy of a series of representative animals in great detail without any particular reference to the physiological significance of the parts described, or any recognition of the fact that anatomy was in its early stages an experimental science. In consequence the educational value of biological study as an introduction to scientific method is reduced to a minimum.

One illustration will suffice to make my meaning clear. The structural basis of nervous co-ordination is a schematisation known as the reflex arc. This, as indicated at length in Chapter III, is based on elaborate experimental analysis as well as on anatomical data. More than three centuries elapsed between the experiments of Vesalius—who first studied the properties of nerve—and the modern conception of the reflex arc as represented by a familiar diagram to be found in any zoological text book. Those who follow the type system slavishly leave the student with the impression that the reflex arc is something which can be actually seen. This is not only regrettable because it is incorrect ; it is regrettable because an examination of the evidence in favour of modern views about the anatomical

basis of reflex action provides excellent material for illustrating the method of an experimental science, and I doubt whether the elementary teaching of chemistry provides better opportunities of doing so. From an educational standpoint I regard it as axiomatic that it is of far greater importance that a student of biology should understand the reasoning which enables us to interpret the path of the nervous impulse in a simple reflex than that he or she should remember technical names for all the branches of the vagus nerve in the rabbit or dogfish. Under the " type system " the universities of England in particular have trained two generations of students who, for the most part, have no clear notion of what is implied by the " nervous impulse " when they have completed their graduate courses in zoology.

American zoologists have broken away from the severely architectural tradition of the Huxleyan type system. The greater influence of biology in American education may be partly due to this. The presentation of biological information in the form of general " topics," as adopted in some American manuals and in one attractive text book recently published in Great Britain, is certainly calculated to enlist the interest of the student. On the other hand, it tends to vagueness and a lack of logical coherence. To make knowledge palatable is important. It is, however, important to do more. As a training in scientific method a succession of logically disconnected themes dealing with different aspects of behaviour, separate systems of organs, economic applications, etc., is hardly more satisfactory than disconnected descriptions of the architecture of a series of separate animal " types." I have ventured to add to the number of existing text books, because I believe that it is possible to present the necessary minimum of data included in an introduction to zoology without losing sight of the logical unity of biological science. Each chapter is based on a

question, and the question is one which naturally arises from the last issue previously dealt with.

I think that the logical background of a course of biology requires much more attention than that of a course in physics and chemistry. If badly taught, there is a real danger not merely of failure to promote the matter-of-fact attitude to life which biological study should instil, but of reinforcing unscientific habits of thought in a domain where detached and disciplined approach is harder to achieve than in physics and chemistry. At the outset the student should be made to realise that biological science, and in particular animal biology, differs from physics and chemistry only in its subject-matter. Its method, the method of science, is identical. That is to say, it treats of objects in the external world : it expresses the relation between them in the most economical way ; and it makes no assumptions which involve *ethical* value. To interpret the phenomena of living matter in the most economical terms we are driven to ask whether the properties of living matter are not manifestations of the same general principles which have been established in the realm of inanimate nature. This is the ultimate goal of all biological enquiry. But living beings differ among themselves ; and biology has to take into account the relation of one type or *species* of living matter to another as well as the relation of living matter in general to dead matter. I have endeavoured to weave both objectives into a coherent account by adopting the historical approach, and I have done so in the belief that the student will not attain to a sense of the challenging quality of scientific thought, unless he realises the steps by which our present knowledge has been reached.

In Part I the elementary facts of the anatomy of the frog and man are arranged with reference to a continuous examination of the characteristics which distinguish living from non-living matter. Our studies of the machinery of

living matter in Chapter VII will lead us to a physical space-time picture of the process of hereditary transmission. In Part II we then turn to the opportunity of using this knowledge as a basis for the interpretation of the diverse manifestations of living matter. It is customary in zoological text books to describe seriatim the anatomy, development and fossil history of the various groups of the animal kingdom. Such a method is adequate for purposes of reference; but the student who is attracted to the study of biology for the intellectual fascination of the problems it presents for solution will find in this method of presentation, if he has already outgrown the phase of stamp collecting, little to stimulate his interest or quicken his enthusiasm. By dealing with the historical development of the evolutionary theory as a preliminary to the discussion of the present status of the problem of species, I have made the attempt to incorporate a survey of the animal kingdom in which the facts are presented not in the form of a catalogue, but as footnotes to the logical construction of an important generalisation.

To the best of my knowledge this has not been previously attempted, and it is not my intention to underestimate the difficulty of the beginner confronted with so much new material. In order to minimise the tedium and bewilderment experienced by the student, especially one who has not studied Latin or Greek, in encountering for the first time a large number of new technical terms, I have adopted in my own teaching a practice which has proved eminently helpful. Each week during the first half of the year a dozen specimens are placed in the laboratory for identification. Each is a duplicate of a specimen in the departmental museum, and the student is allowed to refer to the museum collection for phylum, class, order, genus and popular name of the specimen. In this way unfamiliarity with systematic nomenclature is overcome by the expenditure of a

minimum of effort before the theoretical survey of the animal kingdom is undertaken (Part II, Chapter XI).

Generations of industrious collection and classification of facts elapsed before the problems with which modern biology is concerned could be formulated. Many of these facts have to be assimilated before the problems themselves can be clearly envisaged. I think it is now possible to present these facts in relation to the continuous development of the major problems. Zoology is emerging from a purely descriptive phase into one of experimental enquiry. This does not mean that we can dispense with all the facts that filled the text books of the past generation, but it does mean that the facts have to be presented in rather different perspective. Indeed, I have had the gratification of learning from my students that my lectures had helped them to realise that there really is some point in knowing about the bones of the skull. I confess that I had not reached this conclusion at the time when I could repeat all the foramina of the dog's skull for the purpose of passing the London University Intermediate Science Examination. I am perfectly aware that I am not the first to write a text book with this end in view, and that there exist several introductory works in which the type system has been relegated to its proper place—the laboratory. Nevertheless, I entertain the hope that my own contribution to the reorientation of elementary biological instruction will be welcomed for the special feature to which I have alluded.

This book has been written during my tenure of the chair in Zoology at the University of Cape Town, and in planning what I regard as an adequate introductory course in animal biology, I have been admittedly fortunate, in that Cape Town is the seat of a rich littoral fauna. Sea urchins with ripe eggs are obtainable throughout the academic year, so that at the beginning of his work in the laboratory each student in the first-year course carries out the procedure

for artificial insemination, and himself witnesses the cleavage of the sea urchin's egg up to the gastrula stage. Laboratories remote from the sea can obtain excellent series of slides of segmentation in the sea urchin from the laboratory of Dr. Sigmund (Stuttgart). I have added an appendix which embodies the course in practical work which accompanied these lectures in the University of Cape Town (during 1928). It runs closely parallel with the lectures, and includes many lecture bench demonstrations, a procedure usually adopted in chemical laboratories but rarely in zoology. In this way the student is given some first-hand acquaintance with the experimental principles of the subject without necessitating the extensive changes in laboratory equipment which class work in both dissection and experiment involves. In spite of the difference of approach, I have covered most of the ground which ordinarily comes into an introductory course, the chief omissions being the more polysyllabic aspects of embryology, and descriptive and purely economic zoology. It is reasonable to assume that for details the student has access to a dissecting manual such as that of Marshall and Hurst, or of Gilchrist and von Bonde.

In field-work classes I have always insisted that my own students should make the acquaintance of the common parasites of the types they study. But I regard the life histories of helminthine, insect and protozoan parasites, that fill up so much time in many elementary courses, as out of place. Economic zoology is a specialist subject and should be separated entirely from an introduction to the principles of biology. I do not claim that my own way of teaching is an ideal one, but I do venture to believe that at a time when methods of teaching zoology are undergoing considerable changes it is worth while that those of us who are trying out new methods should place them at the disposal of others. Many, I am aware, will shake their heads at the introduction of so much new and controversial

material into a book of so elementary a character. I have found in teaching that young people are not interested in a dead subject, but they are attracted to what is—like themselves—in a stage of rapid growth; and in my experience the surest way in which to make dull facts palatable is to make them topical. That perhaps is why newspapers are more popular than academic lectures.

To ensure a sound grasp of the principles of genetics, I believe that it is essential for the student to work out examples based on experimental data. A set of problems for solution in connection with the subject matter of Chapter VII are to be found at the end of the book.

To Mr. G. P. Wells, M.A., of University College, London, I must express my very warm thanks for undertaking to revise the manuscript of this book, and see it through the press.

L. T. H.

CONTENTS

PAGE

FOREWORD vii

PART I

THE NATURE OF LIVING MATTER

CHAP.

I. THE ELEMENTS OF ANIMAL BIOLOGY 3

II. THE MACHINERY OF RESPONSE 22

III. THE MACHINERY OF CO-ORDINATION 47

IV. THE SOURCES OF ENERGY OF THE ANIMAL BODY . . 68

V. THE TRANSPORT OF MATERIALS IN THE ANIMAL BODY . 86

VI. THE DEVELOPMENT OF A NEW ORGANISM . . . 105

VII. THE MACHINERY OF INHERITANCE 133

PART II

THE ORIGINS OF LIVING MATTER

VIII. THE EVOLUTIONARY PROBLEM 179

IX. THE PRINCIPLE OF BIOGENESIS 196

X. THE PRINCIPLE OF UNITY OF TYPE 205

XI. THE PRINCIPLE OF SUCCESSION IN SPACE AND TIME . 257

XII. THE PRINCIPLE OF GENETIC VARIATION . . . 291

APPENDICES :

(I) SUGGESTIONS FOR FURTHER READING 313

(II) SUGGESTIONS FOR A PARALLEL COURSE OF LABORATORY CLASS WORK AND BENCH DEMONSTRATION . . 315

(III) PROBLEMS IN GENETICS 318

INDEX 325

ILLUSTRATIONS

TWO EXTREMES OF COLOUR CHANGE IN THE COMMON FROG . . . . . *Frontispiece*

FIG.		*Page*
1.	PARAMECIUM DIVIDING	10
2.	REPRODUCTIVE ORGANS OF THE FROG	12
3.	DIAGRAMMATIC REPRESENTATION OF FERTILISATION AND EARLY CLEAVAGE	13
4.	HUMAN EGG AND SPERM	14
5.	EARLY CLEAVAGE STAGES IN THE DEVELOPMENT OF THE EGG OF FROG OR TOAD	15
6.	GENITAL ORGANS OF MAN	16
7.	TWO TISSUES	17
8.	BLOOD CORPUSCLES OF MAN AND FROG	18
9.	BLACK PIGMENT CELLS FROM WEB OF FOOT OF FROG	23
10.	STAGES IN "EXPANSION" OF MELANOPHORES	25
11.	RELATION OF MUSCLES AND SKELETAL PARTS	27
12.	MICROSCOPIC STRUCTURE OF MUSCLE	28
13.	SKELETON OF A FROG	29
14.	SIMPLE GLAND FROM SKIN OF FROG OR TOAD	32
15.	GLANDS	33
16.	CILIATED COLUMNAR EPITHELIUM FROM THE TRACHEA OF A RABBIT	34
17.	DIAGRAM OF CILIARY MOTION	35
18.	DIAGRAM TO SHOW CILIARY CURRENTS IN THE GILL CHAMBER OF THE MUSSEL	36
19.	GILL OF THE MUSSEL	37
20.	THE VERTEBRATE EYE	39
21.	THE VERTEBRATE EYE IN SITU	40
22.	THE HUMAN EAR	42
23.	DIAGRAMMATIC HALF SECTION THROUGH HEAD OF FROG	43

FIG.		Page
24.	DIAGRAMMATIC REPRESENTATION OF A STATOCYST OF A MOLLUSC OR SHRIMP WITH THREE NERVE FIBRES	44
25.	APPARATUS FOR DETERMINING VELOCITY OF THE NERVOUS IMPULSE	50
26.	MUSCLE RECORD	51
27.	DIAGRAM TO ILLUSTRATE MÜLLER'S EXPERIMENT	54
28.	DIAGRAM TO ILLUSTRATE EFFECT OF SECTION IN NERVE DEGENERATION	55
29.	DIAGRAM OF THE REFLEX ARC	56
30.	EFFECT OF FARADIC STIMULATION OF THE ROOF OF THE MOUTH IN THE CAPE CHAMELEON	*Facing page* 56
31.	BRAIN OF FROG	58
32.	DIAGRAMMATIC REPRESENTATION OF THE CENTRAL NERVOUS SYSTEM OF MAN	59
33.	DIAGRAM TO ILLUSTRATE MOVEMENT OF INSECT TOWARDS THE LIGHT	63
34.	ALIMENTARY CANAL IN THE FROG.	74
35.	ABDOMINAL PORTIONS OF THE HUMAN DIGESTIVE TUBE	75
36.	RESPIRATORY ORGANS OF FROG AND MAN	81
37.	KIDNEY OF THE FROG	83
38.	DIAGRAM OF VEIN SHOWING VALVES	87
39.	PRINCIPAL ARTERIES OF THE FROG	89
40.	MAIN VEINS OF FROG AND MAN	90
41.	THE HEART OF THE FROG	92
42.	PHYSICAL MODEL.	94
43.	THE RELATION OF THE HEART TO THE LUNGS AND TISSUES	97
44.	DIAGRAM OF GILL ARCHES AND HEART OF A TYPICAL FISH	99
45.	CIRCULATION OF A FISH	100
46.	DIAGRAMMATIC REPRESENTATION OF THE OXYGENATION OF THE BLOOD IN FISH AND MAN	100
47.	EMBRYOS OF SHARK, BIRD AND MAN	101
48.	ARTERIAL ARCHES OF REPTILE, BIRD AND MAMMAL	102
49.	MICROSCOPIC SECTION OF THE THYROID GLAND	103
50.	FOUR EMBRYOS OF THE FROG	106
51.	POSTERIOR, ANTERIOR AND DORSAL ASPECT OF THE FROG EMBRYO	107
52.	TRANSVERSE AND LONGITUDINAL VIEWS OF FROG EMBRYO	107
53.	THE EGG OF THE FOWL	108
54.	FORMATION OF THE FOETAL MEMBRANES OF THE CHICK	110

FIG.		Page
55.	THREE STAGES IN THE DEVELOPMENT OF THE MAMMAL	111
56.	THE HUMAN FOETUS IN UTERO	112
57.	EFFECT OF TEMPERATURE ON THE DEVELOPMENT OF THE FROG TADPOLE	114
58.	ONE-EYED TADPOLE	115
59.	AXOLOTL LARVA OF MEXICAN SALAMANDER, BEFORE AND AFTER FEEDING WITH THYROID GLAND	*Facing page* 118
60.	DIAGRAMMATIC REPRESENTATION OF NUCLEAR DIVISION IN A SPECIES WITH FOUR SIMILAR CHROMOSOMES	124
61.	REDUCTION DIVISIONS IN MALE OF A SPECIES WITH FOUR SIMILAR CHROMOSOMES	125
62.	CONTINUATION OF FIG. 61	125
63.	REDUCTION IN THE FEMALE	126
64.	MICROPHOTOGRAPH OF CELL	*Facing page* 126
65.	CHROMOSOMES OF THE STONE-FLY	128
66.	CHROMOSOMES OF THE PLANT BUG PROTENOR	129
67.	CHROMOSOMES OF THE PLANT BUG EUCHISTUS	129
68.	THE MALE AND FEMALE OF THE BANANA FLY	130
69.	DIAGRAMMATIC REPRESENTATION OF THE FIRST GENERATION OF A CROSS BETWEEN THE WILD TYPE OF THE BANANA FLY AND THE VESTIGIAL-WINGED MUTANT	146
70.	CONTINUATION OF FIG. 69	147
71.	CROSS BETWEEN THE "EBONY" AND "VESTIGIAL" MUTANTS OF THE BANANA FLY	151
72.	RESULT OF MATING FIRST HYBRID GENERATION OF AN EBONY-VESTIGIAL CROSS *inter se*	152
73.	FOUR DIFFERENT TYPES OF COMB IN THE DOMESTIC FOWL	153
74.	A SEX-LINKED CROSS	155
75.	RECIPROCAL CROSS OF FIG. 74	157
76.	CROSSING OVER BETWEEN TWO SEX-LINKED MUTANT GENES	161
77.	DIAGRAM TO EXPLAIN CROSSING OVER BETWEEN TWO LOCI ON A CHROMOSOME	162
78.	LINKAGE IN A NON-SEX-LINKED CROSS	164
79.	CROSSING OVER IN THE BLACK-VESTIGIAL CROSS	166
80.	DIAGRAM TO ILLUSTRATE THE LINEAR ARRANGEMENT OF THE GENES	167
81.	MAP OF SOME OF THE MUTANT GENES OF DROSOPHILA	168
82.	NORMAL FREQUENCY CURVE ILLUSTRATED BY VARIABILITY IN WEIGHT OF BEANS	173
83.	CURVES TO ILLUSTRATE MAXIMUM VARIABILITY IN THE SECOND GENERATION	175

FIG.		Page
84.	FIGURE OF THE BARNACLE AND GOOSE IN GERARD'S HERBALL	197
85.	SHELLS OF RADIOLARIA AND FORAMINIFERA	201
86.	THE AMOEBA	202
87.	THE CRAYFISH	207
88.	THE CAPE SCORPION	208
89.	THE LOCUST	209
90.	EYES OF ARTHROPODS	210
91.	GROSS ANATOMY OF RESPIRATORY ORGANS OF ARTHROPODS	214
92.	RESPIRATORY STRUCTURES OF ARTHROPODS	215
93.	DIAGRAMMATIC REPRESENTATION OF AN IDEAL ARTHROPOD	216
94.	THE BARNACLE	218
95.	THE CHITON	223
96.	UNITY OF TYPE IN MOLLUSCA: COMPARISON OF ANATOMY OF CHITON AND A BIVALVE	224
97.	UNITY OF TYPE IN MOLLUSCA: COMPARISON OF A LIMPET AND A CUTTLEFISH	225
98.	CILIATED LARVÆ OF MOLLUSCS: TROCHOPHORE AND VELIGER	226
99.	DIAGRAMMATIC REPRESENTATION OF AN IDEAL ECHINODERM	235
100.	THE GREEN HYDRA	237
101.	HYDRA	238
102.	DIAGRAMMATIC REPRESENTATION OF AN IDEAL POLYCHAETE	243
103.	DIAGRAMMATIC REPRESENTATION OF AN IDEAL FLAT-WORM	245
104.	DIAGRAMMATIC REPRESENTATION OF A POLYZOA AND A ROTIFER	249
105.	TUNICATA	254
106.	THE REMAINS OF A GIANT SALAMANDER	258
107.	THE SUCCESSION OF VERTEBRATES	260
108.	A TRILOBITE	261
109.	ARCHAEOPTERYX	263
110.	CARTILAGINOUS SKULLS OF THE DOGFISH AND THE FROG TADPOLE	265
111.	THE AXIAL SKELETON	266
112.	HEADS OF TWO FOSSIL FISHES	270
113.	THE SKULL OF A PRIMITIVE AMPHIBIAN	271
114.	THE PALATAL AND UPPER JAWBONES OF A STEGOCEPHALIAN	273

FIG.		Page
115.	THE COMPOUND LOWER JAW OF A REPTILE	274
116.	THE CHONDRIAL BONES OF THE MAMMALIAN SKULL	275
117.	THE PENTADACTYL LIMB AND ITS GIRDLE	276
118.	RIB AND STERNUM OF A MAMMAL AND CARTILAGINOUS RIB OF A SALAMANDER	277
119.	COMPARISON OF SKULLS OF REPTILES AND MAMMAL	278
120.	SHOULDER GIRDLE OF A MONOTREME AND TYPICAL MAMMAL	279
121.	HEAD OF HUMAN FOETUS	280
122.	SKULLS OF RHYNCHOCEPHALIAN, DINOSAUR AND MODERN BIRD	281
123.	LIMB SKELETON OF A BIRD	282
124.	DIGITS OF FORE LIMB OF ARCHAEOPTERYX, SIXTEEN-DAY CHICK AND ADULT FOWL	283
125.	DIAGRAM ILLUSTRATING THE RESULTS OF SELECTING FOR EXTRA BRISTLES IN DROSOPHILA MELANOGASTER	298

ACKNOWLEDGMENTS

MANY thanks are due to the Authors, Editors and Publishers of the following works and journals for permission to reproduce the following figures:—A. M. Marshall, *The Frog*, for Fig. 13; Parker and Haswell, *Textbook of Zoology*, for Fig. 95; T. H. Huxley, *Lessons in Elementary Physiology*, for part of Fig. 15 and Fig. 35; Graham Kerr, *Zoology for Medical Students*, for Fig. 85 (all published by Macmillan & Co., Ltd.); E. S. Schafer, *Experimental Physiology*, for Fig. 25; Henry Gray, *Anatomy* (1920), for Fig. 121 (both Longmans Green & Co., Ltd.); *The British Journal of Experimental Biology*, Vol. 1, No. 1, for the Frontispiece; J. Gray, *Ciliary Movement*, for Fig. 17 (both Cambridge University Press); Howell, *Physiology*, for Fig. 42 (W. B. Saunders Co., Ltd.); H. G. Wells and A. M. Davies, *Textbook of Zoology*, for Figs. 52, 53 and 87 (University Tutorial Press Ltd.); J. Johnstone, *Mechanism of Life*, for part of Fig. 15, Figs. 32, 45 and 54 (Edward Arnold & Co.); C. S. Minot, *The Problem of Age, Growth and Death*, for Fig. 57 (John Murray); Gilchrist and von Bonde, *Practical Zoology*, for Figs. 39 and 86 (E. S. Livingstone); *Outline of Science*, for Fig. 22 (George Newnes Ltd.); E. G. Conklin, *Heredity and Environment*, for Fig. 4 (University of Princeton Press); Morgan, Sturtevant and Bridges, *The Mechanism of Mendelian Heredity*, for Fig. 81 (Henry Holt & Co., Ltd., N.Y.); *Kuhenthal and Krumbach's Handbuch der Zoologie*, article by Handbosch, for Fig. 108 (Walter de Gruyter & Co., Berlin); R. Goldschmidt, *Die Lehre von der Vererbung*, for Figs. 64 and 72 (Julius Springer, Berlin); A. W. Grabau, *Textbook of Biology*, for Fig. 109 (D. C. Heath & Co., Boston, Mass.); C. M. Child, *The Physiological Foundations of Behaviour*, for Fig. 58 (Chicago University

Press); H. G. Wells, Julian Huxley and G. P. Wells, *The Science of Life*, for Fig. 106 (Waverley Book Co., Ltd.); and to Messrs. Sidgwick & Jackson, for Fig. 19, reproduced from the Author's *Comparative Physiology*. My special thanks are due to Professor D. M. S. Watson, F.R.S., for Figs. 115 and 116, which he drew specially for this book. Should any acknowledgment have been inadvertently omitted, I trust that my apology for the oversight may be accepted.

L.T.H.

PART I

THE NATURE OF LIVING MATTER

Now, in conclusion, the Method which teaches adherence to the true order and an exact enumeration of the conditions of the thing sought includes all that gives certitude to the rules of arithmetic.—DESCARTES : *Discourse on Method.*

Chapter I

THE ELEMENTS OF ANIMAL BIOLOGY

THE objects with which we are familiar in the world around us may be classified in two main categories, those that we speak of as living matter, and those that we speak of as non-living matter. A piece of chalk or a motor bicycle are examples of non-living matter. A frog or a University Professor are examples of what is called living matter. Men and women are not such things as dreams are made of. They are things you can see and touch and handle just as truly as you see and handle and touch a piece of chalk. Biology is the attempt to apply the matter of fact method that is called science to the study of those objects in the external world which are denoted by the term living matter. Biology is sometimes defined as the study of Life; but it is well to remember that science is not the study of abstract nouns. This characteristic of dealing with facts rather than words differentiates the scientist from the metaphysician, and distinguishes the disciplined, precise and definite character of scientific study from vague, unprofitable and undisciplined discussion. Scientific method has the peculiarity that it preserves the utmost economy; it dispenses with any assumptions that are unnecessary to the building up of those rules or "laws" which enable its votaries to prophesy correctly about the future, and thus achieve a consummation to which mankind has throughout history aspired with conspicuous lack of success when using other methods. Because economy of thought (William

of Occam's principle : *Entia non multiplicanda prœter necessitatem*) is rigorously maintained in any enquiry which is truly scientific, the ultimate goal of biological enquiry is to find generalisations common to the realms of living matter and non-living matter. So at the threshold of our studies we have to enquire into the nature of this conventional distinction. When in the laboratory we see a sheep's heart beating three weeks after the owner is legally dead, we are forced to realise that the adjectives living and dead are used in newspapers and police court evidence in a somewhat loose and arbitrary sense wholly inadequate to a comprehensive treatment of the nature of life.

If we take a piece of chalk as an example of dead matter, it requires no elaborate experiment to show that, provided it is not subjected to great heat or mechanical pressure, it does not display any discernible changes in shape or colour or texture over long periods of time, nor does it increase in bulk or give rise to new pieces of chalk, if left to itself. An animal is different in all these respects. It is constantly changing in shape, position, colour, texture, etc. ; we may say that it has greater *reactivity.* It is influenced by innumerable events to which the piece of chalk remains comparatively indifferent—light and darkness, warmth, gentle pressure, drought, mild electrical stimuli ; we may say that it has greater *receptivity.* Finally the living animal grows and produces other animals like itself ; it has the property of *reproduction.*

1. Reactivity

As the reader reaches this unusual word he may yawn. His face changes in shape. On completing this response, he (or she) may blush. The face changes in colour. As these words are being written the muscles of the writer's arm are changing in shape, and the fingers are changing in position.

Reactivity is the most characteristic feature of the kind of living matter which we call *animals*. Some artificial machines show considerable capacity for effecting changes and very powerful activity which a piece of chalk does not display. But, in general, animals show a greater variety of response than the machines which we do not call living. It is a matter of degree rather than kind.

When we study the reactions of an animal we find that they are for the most part confined to some definite portion of it. They are *localised*. Different portions or organs carry out different types of reaction—movement, emission of fluids, light production, etc. Below is a list of some characteristic reactions of animals and the organs which carry out these reactions. Such organs as the muscles and glands which carry out characteristic changes of behaviour are called collectively *Effector* organs. These organs will be studied in detail later, when the terms will be fully explained:

Type of Response	Effector Organ
Movement	
(*a*) limb, etc.	Striped — *Muscle*
(*b*) gut (peristalsis) bladder (micturition)	Plain — *Muscle*
(*c*) heart beat	Cardiac — *Muscle*
Fluid Motion	
Roof of frog's mouth Gills of clam, etc.	*Ciliated Epithelium*
Secretion	
Flow of saliva Sweating Venoms, etc.	*Glands*
Colour Change	
Chameleon's skin, etc. Retinal pigment cells of Man	*Pigmentary Effectors* (Chromatophores)
Bioluminescence	
Firefly Glow-worm	*Photogenic Organs*

II. Receptivity

When an animal responds in any of the characteristic ways which have been enumerated above, it can generally be found, if sufficient trouble is taken, that the response is related to some definite happening in its surroundings, to some physical event in the external world. The reader perhaps yawns once more as he reads this: the yawn (if it occurs) is definitely related to the words he is reading; careful study would show that in similar circumstances he (or she) would not yawn, if the written matter announced a legacy of £5,000 to himself or herself. As an illustration of the dependence of an animal's behaviour on its immediate surroundings one may take the power of colour change in the frog. Like the chameleon the frog exhibits changes of hue; but they are not so rapid. Indeed they require periods of several hours rather than minutes to reach completion; though they are just as striking. Colour response in the frog is influenced by three principal external influences—light, moisture and temperature. If the field of vision is occupied by a light-scattering surface ("white background") the animal will be paler than if the field of vision is occupied by a light-absorbing surface ("black background"); if kept dry the animal will be paler than if it is kept in water; and at 22° C. it will be paler than at 5° C., other factors being constant. So the optimum conditions for pallor are white background, dryness and warmth; while for darkening of the skin, black background, moisture and cold are best.

The chameleon like the frog responds to light and temperature, and it will become completely pale after suitable electrical or mechanical stimulation. A toy shocking-coil serves well for the former purpose. If we apply these stimuli to the different regions of the body we find that the same stimulus does not always call forth the same

colour changes. Thus if the skin of the surface of the body, roof of the mouth, and excretory orifice (cloaca) are respectively stimulated by a series of electric shocks, or by hard rubbing with a glass rod, the results obtained may be tabulated thus :—

COLOUR CHANGE IN THE CHAMELEON

Stimulus	*Area*	*Response*
Electrical	Skin of surface	Local pallor
	Roof of mouth	Generalised pallor
	Cloaca	Generalised pallor
Mechanical	Skin of surface	No effect
	Roof of mouth	No effect
	Cloaca	Generalised pallor

In the case of the chameleon light acts on any portion of the skin, making dark (not pale) the area on which the light falls. This is not the case with the frog or with fishes, many of which respond in a very striking manner to light and darkness. Blinded or blindfolded fish do not respond like fish in which the eye is perfectly intact and accessible to the light. This is true also of the frog, but because colour response in the common frog is influenced powerfully by temperature and moisture, the part played by the eyes can be better illustrated in one of its near cousins, the South African clawed toad (*Xenopus lævis*) which lives in water and is much less susceptible in this respect to the influence of temperature. When the skin colour of clawed toads is compared under different conditions of illumination, the contrast of normal and eyeless or blindfolded individuals is as indicated in the following table :—

COLOUR CHANGE IN XENOPUS LÆVIS

	White background	*Black background*
Normal animal ...	Very pale	Very dark
Eyeless animal ...	Intermediate	Intermediate

We see from this that just as different portions of the body, the effector organs (muscles, glands, the " pigment cells "

which are responsible for colour changes like the above, etc.), are specially concerned with carrying out responses, so special parts of the body (*receptor organs*) are specially affected by the various happenings in the animal's surroundings which call forth response of one kind or another. The term *receptor organ* replaces the older one *sense organ* in contemporary biological nomenclature. It is greatly to be preferred, for it involves no departure from our initial resolve to treat the animal as a physical object of the external world. The term sense organ involves a habit of speech which is foreign to a physical science, and there is no reason to perpetuate it in the early stages of biological study. For the same reason the term *purpose* should never be used in biology. An *organ* fulfils a certain *rôle* in the economy of the organism. Whether it discharges a purpose we cannot know by any methods whose validity has been vindicated so far. Thus the eye is the main receptor organ through which light influences the behaviour of an animal. In our own case the ear is the organ by which sound vibrations exercise an effect upon us. The ear is a complex organ, and is also the structure by which gravity operates on our behaviour. Some important receptor organs which will be dealt with in a later chapter are given in the list following :—

Type of Stimulus	Receptor Organ
Light	*Retina*
Sound	*Cochlea of Ear*
Gravity (mechanical displacement)	*Labyrinth of Ear*
Chemical	
(*a*) Gaseous	*Olfactory Membrane*
(*b*) Dissolved	*Gustatory Membrane*
Deep Mechanical Pressure	*End Organs in Muscles*
Temperature	*End Organs in Skin*
Generalised Superficial Pressure	*Tactile Bulbs in Skin*

The power of receptivity is not peculiar to animals in any absolute sense. We can make machines which will respond

to any type of stimulus. A device which responds to light by movement is seen in the windows of any large optician. Animals, however, excel in receptivity even the most complicated of the machines which man has so far devised.

III. Reproduction

Reproduction is not a property possessed by all living matter; nor even by all the units of living matter which we call individuals, as met with in nature. The worker bee does not reproduce its kind, but the worker bee could not have existed if there had been no other bees. Every piece of living matter we know has been manufactured by some other piece of living matter very much like itself. The Ford car, like the frog, has a movable body; but we do not see little Ford cars disporting on the grass before the garage. Most artificial machines are made to-day by the activity of other artificial machines; but the machines which co-operate to make a Ford car are not themselves Ford cars or very much like Ford cars. With animals it is a universal rule that *like begets like*. This now commonplace statement has only been known to be true of all animals for about a hundred and fifty years. The history of our knowledge of the reproductive process in animals will be set forth later.[1]

Animals produce other animals in two different ways. One way is called asexual, and the other, which requires the co-operation of two animals, respectively called the male and female, is called sexual reproduction. The first is a much simpler method, less unlike processes which we can imitate artificially. It is the only method of reproduction in large numbers of minute organisms which are simpler in their organisation than any of the things we ordinarily call animals or plants, as the germs of disease and putrefaction

[1] Chapter IX.

(bacteria). Asexual reproduction does not occur in the more complex animals like frogs or ourselves.

Asexual Reproduction. As an illustration of the latter, therefore, we shall have to study one of the small organisms that can usually be found in mud. If samples of mud from several ponds are added to a little pond water in which a few bread crumbs have been allowed to soak, after standing

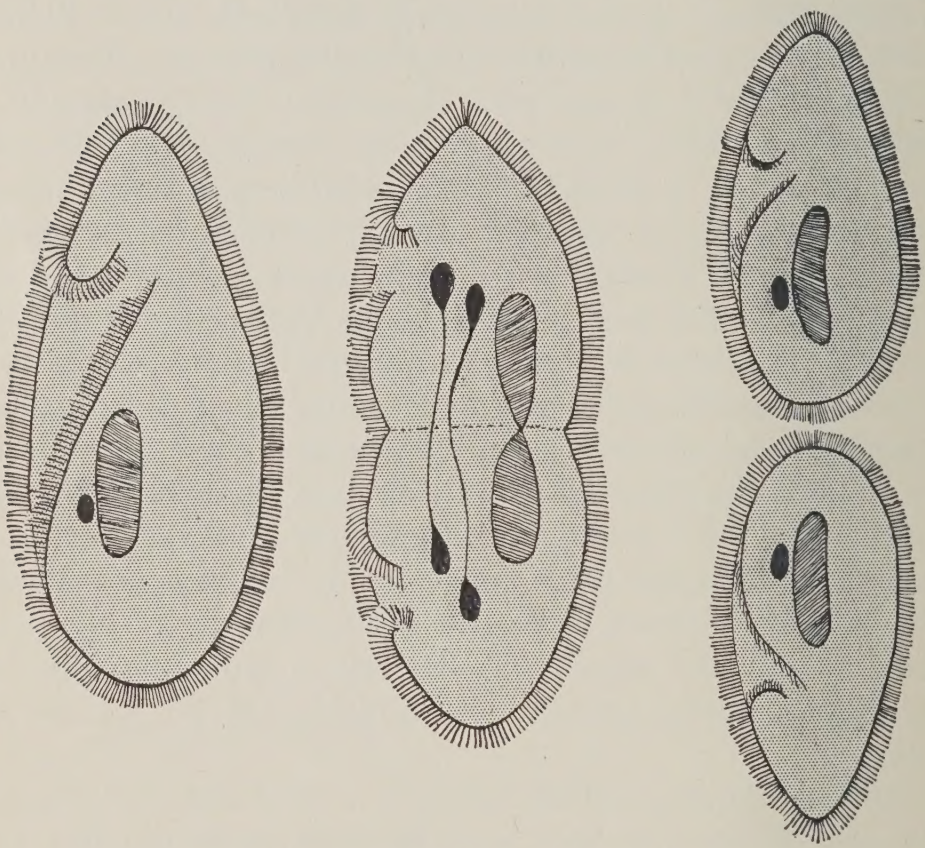

FIG. 1—PARAMECIUM DIVIDING

for about a day or two the mud at the bottom when examined under the microscope is found to contain little rapidly moving creatures, denoted by the technical name, *Paramecium.* Each is of a cigar shape, and if you can observe one when it is not moving too quickly you will see that its movements are due to fine flickering processes called *cilia* (because of their resemblance to eyelashes—

the Latin word). These cover the whole body. Somewhat similar organisms (Opalina, Balantidium, etc.) can always be found living parasitically in the muddy contents of the hindermost portion of the bowel of the frog. When such organisms as these have gone on feeding for a certain time, they become constricted about the middle, and gradually divide into two, just as a drop of a fluid will divide into separate drops when it has reached a certain size. (Fig. 1.) Each half becomes a new individual and swims off on its own. Thus every Paramecium arises from another Paramecium. *Like begets like* is a rule that applies equally to Paramecium, the common frog and ourselves. But in all those organisms which are properly called animals in every-day language each sort or *species* has two kinds of individual, males and females; and reproduction involves the co-operation of a male and a female. Both are equally essential to the production of a new being, though the precise part which the male plays in the process was not clearly understood till about fifty years ago.

Sexual Reproduction. The female frog differs from the male in its somewhat larger size. At the breeding season, in Spring, frogs will be found in ponds and streams in pairs, a male tightly clasping a female about the body by its fore-limbs, with its ventral surface in contact with her back. Thus they remain, till the eggs are laid. These are shed in great numbers embedded in masses of clear jelly, which may be seen floating on the surface of the water. Each egg is almost completely spherical, black in colour towards the pole which floats uppermost, but lighter beneath. As the eggs are laid the male squirts a viscid stream, the seminal fluid, over the surface of the egg.

If the seminal fluid is examined with a microscope, as was first done by a Dutch draper, Leeuwenhoek, in 1668, it is seen to swarm with minute moving objects, called spermatozoa, or more shortly sperms. When examined with

a very high magnification each sperm is seen to be in shape somewhat like a tadpole, having a short thicker body with a thin whip-like tail or cilium by whose lashing movements the sperm dashes hither and thither. If the male is taken away from the female before the eggs are laid, and the latter removed from the body of the mother, the eggs will not develop into tadpoles. But if these eggs are placed in a bowl of water to which some seminal fluid obtained from a male

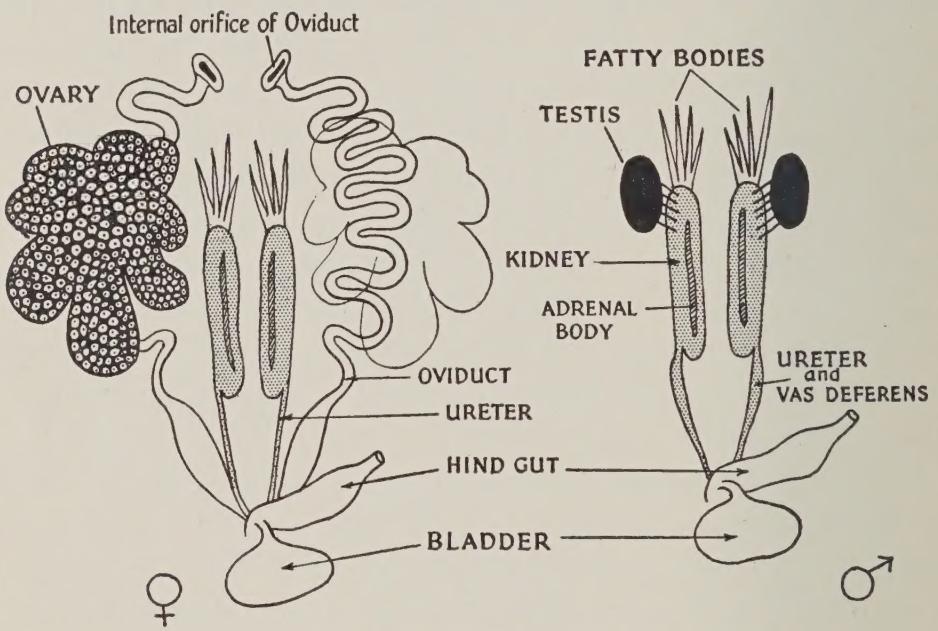

FIG. 2—REPRODUCTIVE ORGANS OF THE FROG

Position of left ovary indicated in outline only.

was added immediately before, they become capable of developing. Towards the end of the eighteenth century the Abbé Spallanzani showed that seminal fluid from which the sperm had been filtered off does not possess this fertilising power, and a century later two German investigators, Hertwig and Fol (1879), observed under the microscope the fact that one sperm, and one only, bores its way into the egg of a sea urchin, as the preliminary to its development into a new organism. We now know this to be true of all animals that reproduce sexually. Development of the egg starts when

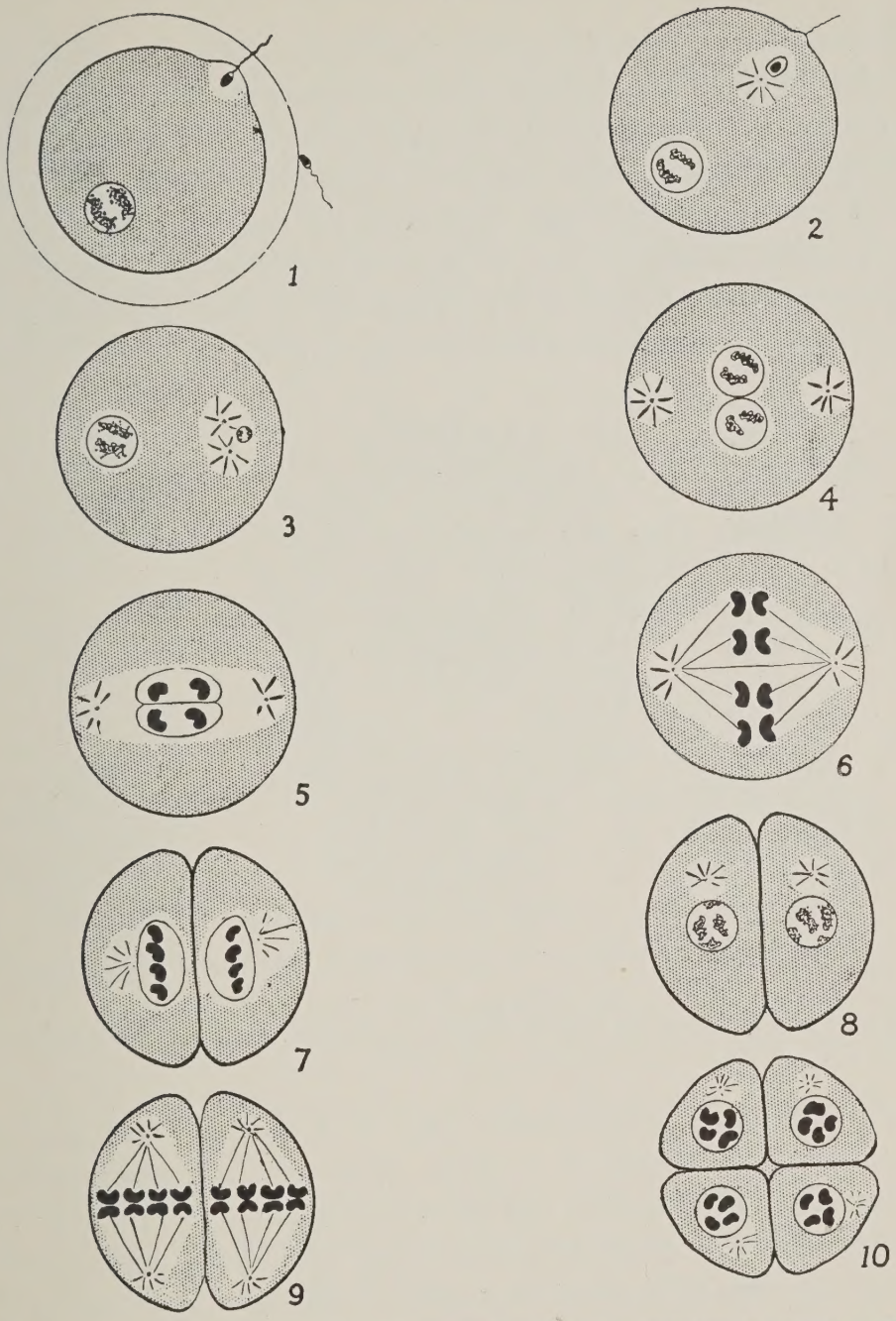

FIG. 3—DIAGRAMMATIC REPRESENTATION OF FERTILISATION AND EARLY CLEAVAGE

In (1) is seen the penetration of the sperm and the formation of the fertilisation membrane, which prevents the entry of other sperms; (2) and (3) show the swelling of the sperm nucleus; (4) and (5) the union of the sperm and egg nuclei; (6) to (10) display the nuclear phenomena which accompany the division of the egg into cells; (8) two-cell stage; (10) four-cell stage. The nuclear changes shown in (5)—(10) are fully explained in Chapter VI.

one of the innumerable minute sperms contained in the seminal fluid ejaculated by the male penetrates into the substance of the egg. *Fertilisation*, the process by which the egg starts to develop into a new creature, is, in all animals, the union of a sperm with an egg. All that we mean by inheritance from the father is due to the material substance of the sperm; all that we mean by inheritance from the mother is due to the material of which the egg is composed.

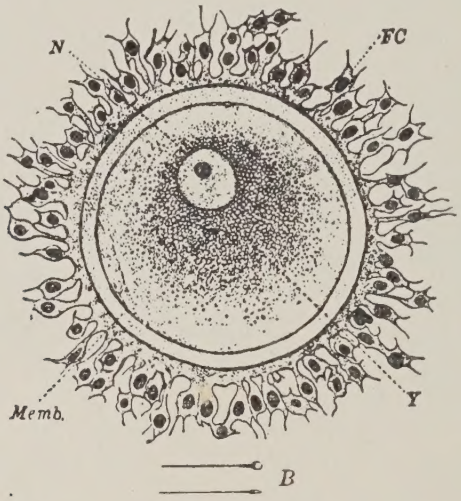

FIG. 4—HUMAN EGG AND SPERM

Above—Egg (ovum) N, nucleus; Y, yolk granules; Memb., egg membrane; FC, follicle cells.

Below—(B) two sperms: the thickened "head" contains the nucleus.
The actual size of the ovum is about 0.2 mm. in diameter and the sperm is drawn to the same scale.

An animal that produces eggs is a female; an animal that produces sperm is a male. The eggs are produced in masses, which are called *ovaries*, within the body of the female. The sperm are produced in a slimy secretion, the seminal fluid, by organs known as *testes*. Collectively ovaries and testes are referred to as *gonads*. Some animals shed their ova or seminal fluid, as the case may be, into the water in which they live. In the case of the frog the male squirts seminal fluid over the eggs as the female lays them. In the female frog the ovaries occupy a large part of the body

cavity in the trunk region; they are masses of eggs in different stages of growth. Two coiled white tubes (*oviducts*) on either side convey them to the exterior, opening along with the excretory orifices by a short tube, the cloaca, between the legs. In the male there are two whitish bodies of ellipsoidal shape—the testes—lying over the kidneys and communicating with the exterior by the same duct or passage which conveys the urine to the common

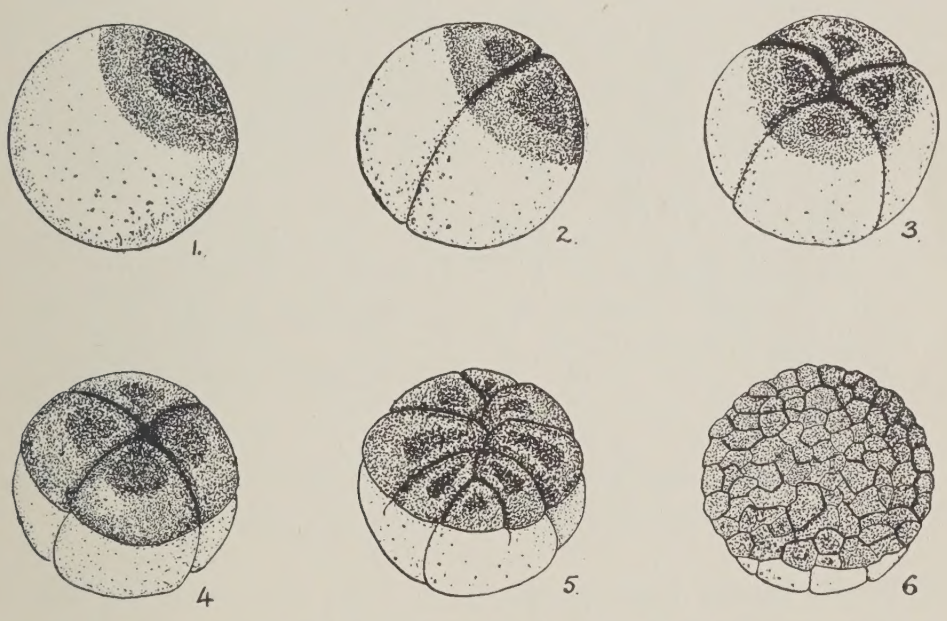

FIG. 5—EARLY CLEAVAGE STAGES IN THE DEVELOPMENT OF THE EGG OF FROG OR TOAD

2, the two-cell stage; 3, the four-cell stage; 4, the eight-cell stage.

excretory orifice. (Fig. 2.) At the breeding season, when the eggs in the ovaries are ripe, it is possible to remove them from the body. If kept in clean water they will not develop, unless, as stated, a drop of seminal fluid, which can be prepared by crushing up the testes of a male, is added. In the frog, as in all animals which reproduce sexually, the egg begins to develop when a single sperm penetrates it.

The sperms of nearly all animals are very much alike

and always of microscopic dimensions. Eggs on the other hand vary greatly at the time of fertilisation. The human ovum is not as large as a pin's head—just visible to the eye. An ostrich egg weighs several pounds. Very young eggs of different animals—eggs from the ovary of a young animal for instance—are strikingly alike. In many animals such as snails, human beings and birds, the seminal fluid is introduced into the oviduct of the female and the egg is

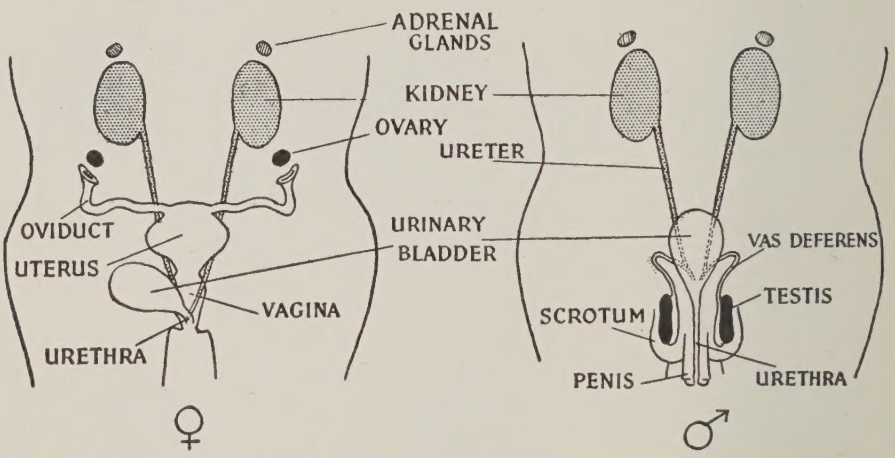

FIG. 6—GENITAL ORGANS OF MAN WITH ASSOCIATED STRUCTURES
On the left, female (♀); on the right, male (♂).

fertilised inside the female body. In the fowl the egg is fertilised shortly before it enters the oviduct, and in its passage through the latter the essential part of the egg, the yolk, acquires a slimy coating, the albumen or white, and a chalky shell. In some animals the male has a special organ, the *penis*, which is used to introduce the seminal fluid into the body of the female. (Fig. 6.)

The female frog lays her eggs embedded in masses of a clear jelly, analogous to the albumen of the fowl's egg. But they have no shell. So we can study what follows fertilisation more easily in the frog than in an animal whose eggs are protected by an opaque envelope or develop to a late stage in the body of the mother. Once the sperm has made

its way into the egg a change occurs so that no other sperm can penetrate it. Soon after a furrow appears on the surface of the egg, which divides into two in much the same way as a Paramecium divides in asexual reproduction. But the two halves, which are called *cells*, do not separate, like two newly-formed Paramecia, to start separate lives of their own. They remain connected and divide again. The process is repeated until, within twenty-four hours after

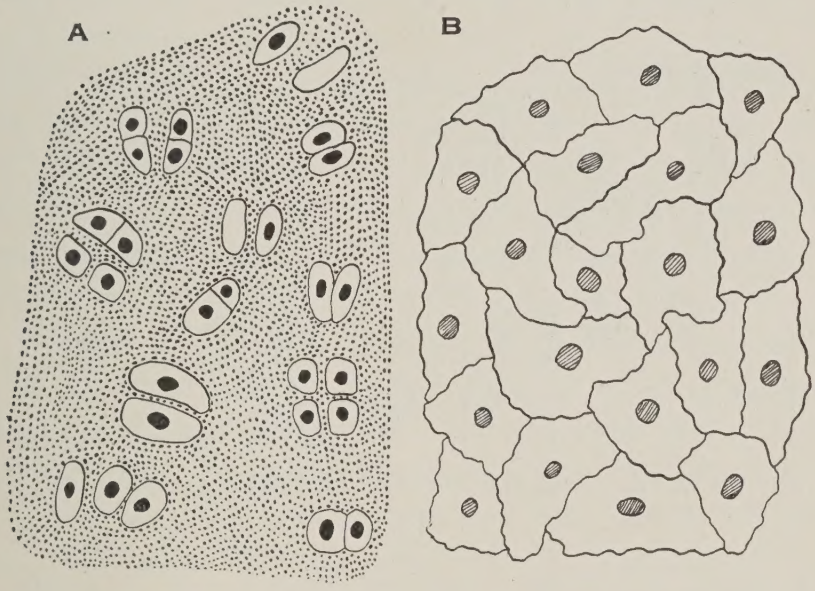

FIG. 7—TWO TISSUES

A. Cartilage (matrix dotted) from shoulder blade of Frog.
B. Epithelium from wall of abdominal cavity of Mammal.

fertilisation, the black egg can be distinctly seen with a simple lens to be a hollow ball of such cells. Then occur changes in the rate of multiplication of the cells in different regions, and from different groups of cells the various structures of the body begin to take shape.

The Cellular Structure of the living body. The cells of the body, which are all alike at first and resemble a very small egg from the ovary, are the microscopic bricks of which the whole edifice of the body is constructed.

The cells of different parts of the body in the tadpole or adult frog are not all alike in size or shape. But they all resemble one another in possessing a structure known as the nucleus, which is very prominent as a clear spherical body in the immature eggs. When cells divide, the nucleus divides in a very characteristic way, which we shall study later. The testis, like other organs of the body, is seen under the microscope to be composed of cells ; and its cells are constantly dividing to provide new sperm. For each sperm is formed

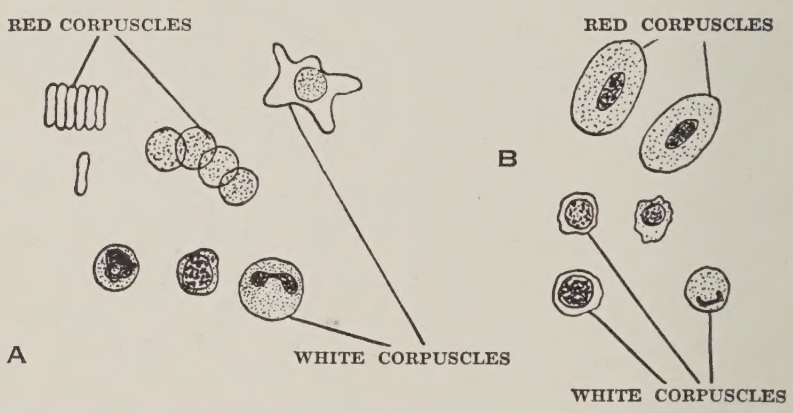

FIG. 8—BLOOD CORPUSCLES OF MAN (A) AND FROG (B)

from a single cell of the testis, the body or thick portion of the sperm being the nucleus. In a similar way, eggs are produced by cell-division in the ovary. The development of a sperm from a single cell of the testis was first shown by Kölliker in 1841. When, at fertilisation, the sperm penetrates the egg, the tail or flagellum is either sloughed off or absorbed. The body or nucleus swells up and unites with the nucleus of the egg in preparation for the first segmentation division. (Fig. 3.)

Like the testis or ovary, the substance of all the organs of the animal body is built up of microscopic bricks which we have called cells. In some tissues like bone and cartilage the bricks are separated by a good deal of plaster, or to use

the technical term, *matrix*. Others, such as the *epithelia* or lining membranes of all surfaces, internal or external, including the tabular cavities of the glands, consist simply of cells packed closely together. As we shall see later, the cells of different tissues are, as development proceeds, considerably differentiated. But they all arise by division of undifferentiated cells in the course of development, and the process of cell division involves the partition of the nucleus in that highly characteristic manner, described under the term *mitosis*, in Chapter VI.

Some animals have eggs with a large amount of food stored in them. The fowl's egg affords an example of this. After the sperm nucleus has united with the egg nucleus—(visible to the eye as a white speck in a clear circular area on the side of the yolk in the unfertilised fowl's egg)—the combined nucleus divides in the usual way, but only a small part of the fowl's yolk is partitioned off round each cell ; so the embryo is at first a small plate of cells lying on the surface of the remaining yolk and growing at its expense. The domestic fowl lays eggs at definite intervals—in high-laying strains like the White Leghorn about twenty-six hours. The eggs are deposited whether they are fertilised or not. In the human female an egg is liberated into the oviduct once a month, after sexual maturity is reached (about the age of thirteen). The process is associated with a regular renewing of the mucous membrane of the internal generative passages, accompanied by a slight hæmorrhage.

The Physical Nature of Fertilisation. The entry of the sperm is a physical event associated with material changes in the egg, and these changes are capable of being imitated. One of these changes is an increase of permeability to dissolved substances ; and physical agents which change the semi-permeable property of the egg periphery are capable of initiating the process of cleavage without the aid of the sperm. Jacques Loeb discovered in 1899 that by

placing eggs of the sea-urchin Arbacia in a mixture of sea water and magnesium chloride about twice the molar concentration of sea water, a large proportion grew into free swimming larvæ. Later, he found that this was not due to the specific action of magnesium, since sea water made more concentrated with a variety of substances would do exactly the same. Moreover, the concentration of each substance which was most effective, *i.e.* produced the greatest number of successes, was found to be such as to exert a definite *osmotic pressure*, *i.e.* to have a corresponding power of withdrawing water from the egg. Subsequently Loeb found that by preliminary insertion of the eggs in acidified sea water, a hundred per cent. fertilisation could be obtained. Again, the strength of acid is related to the ease with which it will pass through the fatty outside layer of the egg. *Artificial parthenogenesis* by various methods has now been perfected in many groups of the animal kingdom. Bataillon developed a method of mechanical pricking of the Frog's egg; and fatherless tadpoles have actually been raised through the metamorphosis stage to the adult condition.

Immediately after fertilisation another important change occurs in the egg. All the while it is, in popular language, "alive," that is all the while it retains its capacity for developing further, the egg can be shown by that delicate electrical thermometer, the thermopile, to be giving off heat. It can also be shown, by chemical analysis, to be steadily taking up oxygen and giving off carbon dioxide gas. Immediately after the penetration of the sperm or artificial activation, the heat production and oxygen intake suddenly increase, sometimes a thousand-fold in a few minutes. We call this activity respiration, and have hitherto regarded it as inseparably bound up with the other properties we refer to, when we say the egg-cell is alive. We can nevertheless study it apart, just as we can study the

development of the sea urchin egg without the aid of the sperm. Warburg (1912) showed that, if sea urchin eggs are suddenly dried by plunging them in acetone, and subsequently powdered, this powder when moistened can continue to take up oxygen for some time, like the egg-cell, and those poisons which act by stopping respiration in the tissues of an animal, such as cyanides (prussic acid salts) affect it in just the same way. Warburg found further that the action of prussic acid was definitely related to the amount of iron in the egg cell, and that suspensions of charcoal containing traces of iron will induce fatty substances, sugars and the products of substances like egg white to undergo slow combustion in air. These iron-containing charcoal suspensions are also affected by cyanides in the same way as living cells ; that is to say, minute traces of prussic acid salts will bring their power to facilitate oxidation of organic substances to a standstill.

Here the student would do well to ponder again upon the meaning of the term *alive*. A century ago the Abbé Spallanzani showed that when luminous jellyfishes are desiccated and ground to powder the powder will at once emit light when moistened. Nobody recognised at the time that a property hitherto associated with " living matter " had been taken over into the domain of chemistry and physics by that simple experiment. We are far from being able to manufacture a system that would be called by any ordinary person " living," but every year shows more striking advances in manufacturing systems which are similar in some respect to what we call living things. The belief naturally gains ground that the characteristic features of the things we call living differ in complexity rather than in kind from the processes of dead matter.

Chapter II

THE MACHINERY OF RESPONSE

WE have enumerated some of the most characteristic differences between animals and non-living objects under three headings: reactivity, receptivity and reproduction. At the conclusion of the last chapter we made a preliminary study of the phenomena of development associated with the property of reproduction. To follow the course of development more closely we need to know more about the architecture of the full-grown animal; and as a starting point we shall retrace our steps to what has already been said about the variety of responses of which animals are capable, and proceed to examine in greater detail the portions or organs of the body concerned with carrying out these responses.

1. The Effector Organs

The effector organs which will be dealt with are: (1) the *pigment cells*, which are responsible for changes in bodily colour in any animal like the frog; (2) the *muscles*, which are responsible for changes in shape and position; (3) the *glands*, which produce fluid materials; and (4) *ciliated epithelium*, whose activity will be explained later.

(1) *Colour Response.* Between the toes of the frog is a thin translucent web, which permits us to make direct observations on what happens when the animal changes from a

pale to a dark hue or vice versa. We can take a frog that has been kept for some hours in a cold, dark room under water and transfer it to a dry receptacle in a warm, well-illuminated situation, and watch precisely what occurs in the skin during the process of transformation from a dark, almost black, tint to the pale yellowish hue which it finally assumes in the latter surroundings. Even with a good hand-lens we can see that the web is flecked with minute spots of blackish colouring matter or pigment. Closer

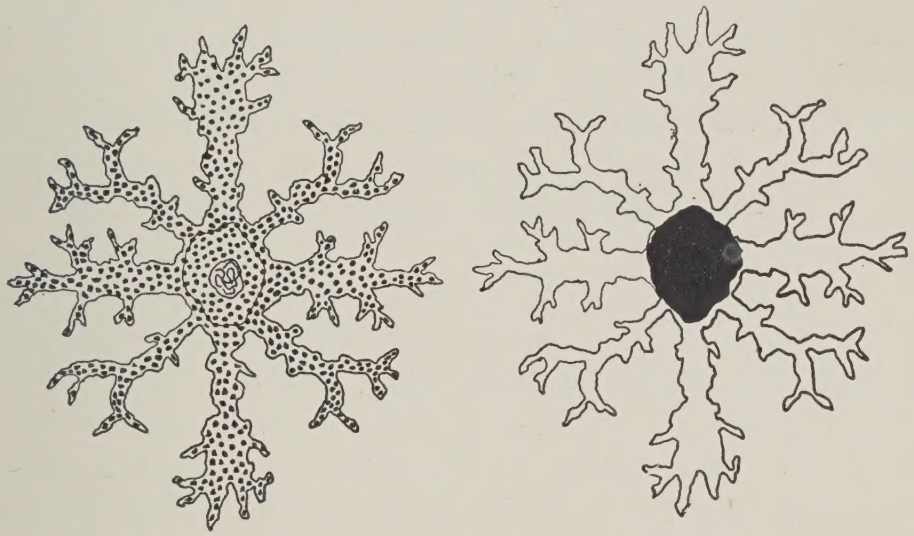

FIG. 9—BLACK PIGMENT CELLS (MELANOPHORES) FROM WEB OF FOOT OF FROG

A Expanded state, i.e. pigment granules dispersed. B Contracted state, i.e. pigment granules aggregated at centre of the cell. A is from a dark, B from a pale, animal.

observation with the low power of a microscope shows that in the completely pale animal each pigment spot is of rounded contour, but that in the intermediate condition it is star-shaped. (Fig. 9.) In the dark animal each pigment spot becomes a rosette of fine threads of pigment interlacing with those of adjacent ones. The changes in colour of the skin of the frog—and the same is true of the skin of the chameleon—are due to the way in which the pigment

is distributed in the skin. Each pigment spot in the pale animal is the centre of a profusely branching cell with a nucleus of its own. When the skin is dark, the pigment is found to be distributed through the whole length of the ramifying processes of the pigment cell, or, to use its technical name, *melanophore*. As the animal becomes paler the pigment is gradually withdrawn along the cell processes until it is finally concentrated in a single compact speck at the cell centre. The melanophores, therefore—as first shown by Milne Edwardes (1848)—are the effector organs of colour response. Colour response in the frog, in the chameleon and in fishes depends on the presence in the skin of certain branching cells which possess the peculiarity of containing a mobile colouring matter or pigment that migrates under appropriate stimulation along their cell processes.

The state of the melanophores, as seen in the thin web of the frog's foot, gives us a much more satisfactory means of studying the effect of external conditions on colour changes than does reliance on the tint of the animal, partly because the tint of two animals at the same extreme of pallor or darkening is never quite identical, and also because small differences in the configuration of the pigment granules are more easy to recognise than slight changes in the tint of the skin. The point may be illustrated by some experiments on a near relative of the frog, the clawed toad Xenopus, to which we have alluded in the previous chapter. It is true that we cannot assess the shape of a melanophore with the precision with which we can measure the tension exerted by a muscle, but we can analyse the response of a clawed toad to light by assigning arbitrary numerical symbols to different stages in the withdrawal or extension (contraction or expansion) of the pigment in the melanophores, as indicated in Fig. 10. In biology as in all branches of science, when we can reduce a problem to quantitative measurement, we are

in a position to predict with some assurance what will happen in a given situation. This is true with regard to the present issue. Observation of a large number of toads placed in containers with black and white sides in dim and bright light

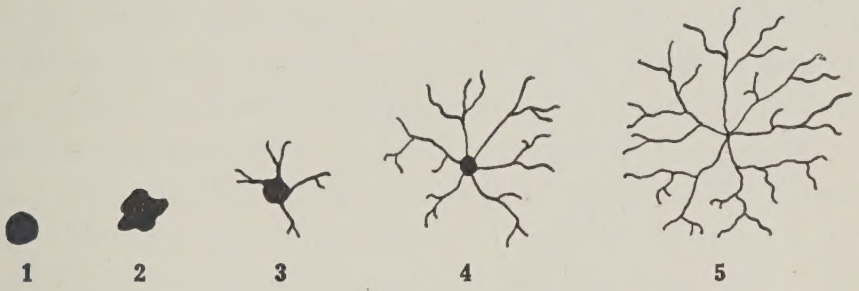

FIG. 10—STAGES IN "EXPANSION" OF MELANOPHORES (*see* text)

gives rise to the impression that the optimum condition for pallor is afforded by placing the animals in a white container dimly illuminated from above, while a black container brightly illuminated from above is the optimum condition for darkening in Xenopus. The significance of this seemingly paradoxical result is at once evident, when we record, in the manner indicated above, the extent of melanophore expansion in series of normal and eyeless toads placed in white or black containers in dim and bright light. In the table given below the mean value for each series and the probable error of the mean value are cited.

COLOUR CHANGE IN XENOPUS LÆVIS

	White Container		*Black Container*	
	Dim Light	*Medium Light*	*Dim Light*	*Medium Light*
Normal Toads...	1.65 ±0.16	2.0 ±0.0	4.25 ±0.15	4.6 ±0.13
Eyeless Toads...	2.75 ±0.18	3.13 ±0.3	2.75 ±0.23	3.0 ±0.31

The examination of these figures shows that there is a slight tendency of the melanophores themselves—independent of the eyes—to become more expanded in bright light. This change is in the same sense as the characteristic response of the chameleon to light, a response which is also independent of the eyes, since it occurs in both normal and eyeless animals. Thus the response of normal toads is due to two components, a primary or direct reactivity of the melanophores themselves, and a secondary more sensitive response depending on whether the field of vision is occupied by a light-absorbing or light-scattering surface. In dim light the primary reactivity reinforces the secondary response to a light-scattering surface, while in bright light the primary reactivity reinforces the secondary response to a light-absorbing surface.

The same experiment can also be carried out with the English common frog, but in that case it is found necessary to keep the temperature constant and perform the experiment wholly under either dry or wet conditions, or alternatively to make a comparison of the results obtained in dryness and in water at a constant warm and a constant cold temperature, leaving the animals for about a week to attain complete equilibrium. Pickle jars coated on the outside with white or black enamel, and covered with muslin are convenient for the purpose.

(2) *Muscular Movement.* When we remove the skin in the region of the jaw or around the limbs, we find fleshy bodies attached at their extremities by tough material called "tendon" to the joints. These fleshy masses or muscles on being teased are found to consist of fine fibres arranged in parallel series, and beneath the microscope the fibres are seen as cylindrical objects with characteristic striations. Each fibre of *striped muscle* (Fig. 12), as it is customary to call the elements of the skeletal muscles (those attached to the skeleton or hard parts of the body),

is derived in development from a single cell. But the nucleus multiplies without division of the cell body, so that the adult muscle fibre, which, though microscopic in girth, may be several inches in length, is eventually multinucleate. On flexing the arm, we notice that the muscles become shorter and thicker, because each fibre increases in thickness as it shortens in length. This shortening pulls on the bone or other hard part to which it is attached. A clear conception of this very elementary fact is a comparatively modern discovery. Vesalius, the pioneer physiologist of the Renaissance, first clearly enunciated the idea that movement of the limbs was specifically due to a change in the fleshy portion or muscles, in his epoch-making *Fabrica Humani Corporis* (1543). It was not until the invention of the microscope that the nature of the muscle fibres could be studied. It was as late as 1662 when Glisson showed that when muscle contracts, a change in shape, not as previously believed of bulk, occurs in each fibre.

FIG. 11—RELATION OF MUSCLES (shaded) AND SKELETAL PARTS (black)

A, Human forearm; B, Leg of an insect.

Muscles of the kind that consist of cylindrical fibres showing well-marked striations are concerned with the movements of the outside of the body, and are generally attached to some hard material which is called skeletal tissue. In an insect they are attached to the horny outer covering of the body, which is divided up into separate segments or joints with thinner more flexible tissue between them serving as hinges (Fig. 11). In the frog and in ourselves, the

skeletal tissues are internal and form a number of separate bones hinged by a tough fibrous material or tissue of whitish colour known as *tendon*, which also serves to bind the ends of the muscles to them.

The *skeleton of the frog* (Fig. 13) may best be described under four headings : the head skeleton, the visceral skeleton,

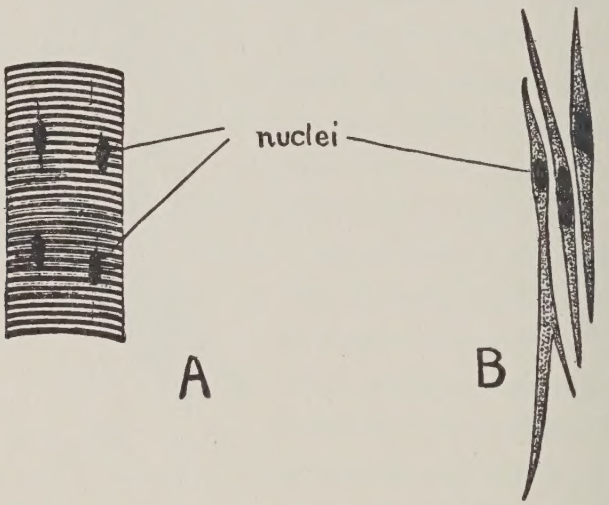

FIG. 12—MICROSCOPIC STRUCTURE OF MUSCLE
A, Part of a striped muscle fibre ; B, Three plain muscle fibres.

the appendicular skeleton and the axial skeleton. The head skeleton or *skull* consists of a protective case for the brain, partly composed of bone and partly of gristle or *cartilage*, and the jaws which provide rigid levers for the muscles that open and close the mouth. The *visceral skeleton* or *hyoid* apparatus is a series of cartilaginous elements to which the muscles that are concerned in the movement of breathing are in part attached. They are the remains of the supporting arches of the gills in the tadpole. The *appendicular skeleton* includes the limbs and their attachments to the trunk (the limb girdles). The names of the principal bones of the fore and hind limb are disclosed in the accompanying illustration (Fig. 13). The *axial skeleton* or *vertebral column* consists of a series of bones,

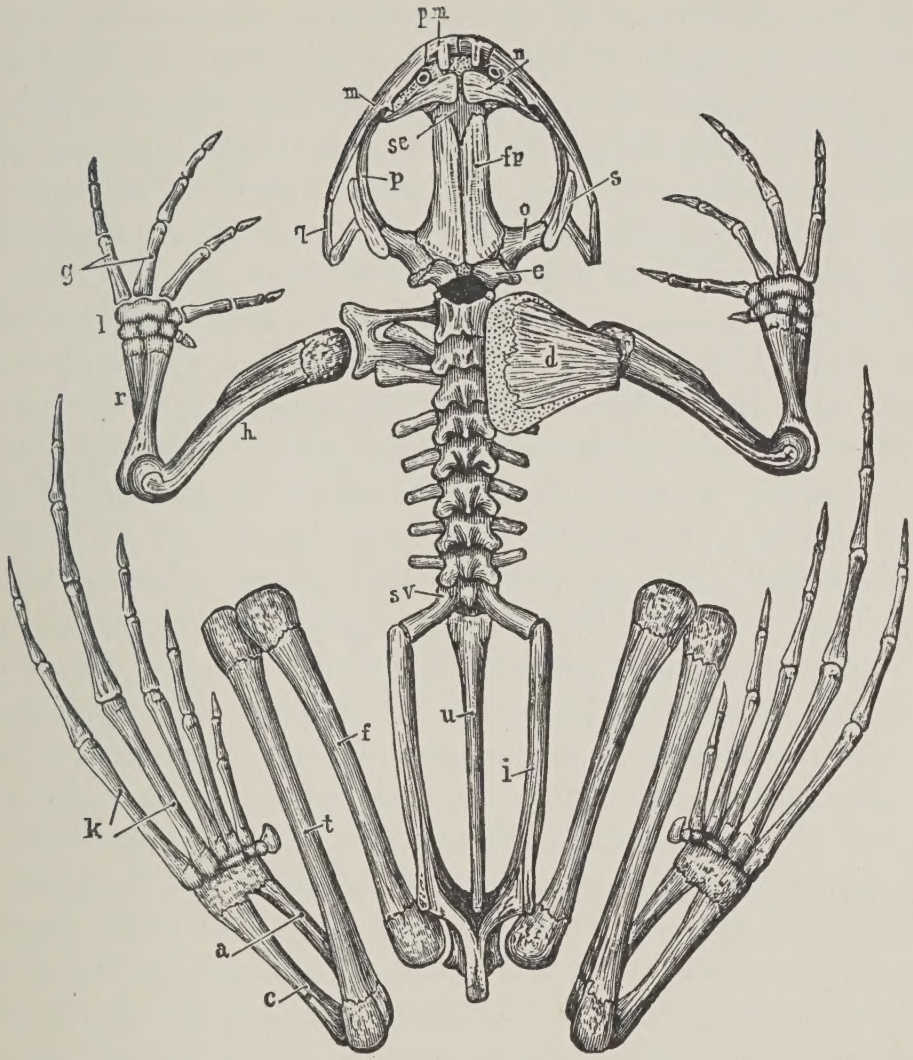

FIG. 13—THE SKELETON OF A FROG (*from* Marshall)

Note the skull, with cranium (fp), auditory capsules (o), nasal capsules (n), jaws (m, q, p) orbits (between cranium and jaws); backbone composed of nine separate vertebræ, and a rod (u) representing several vertebræ fused together; shoulder-girdle (the shoulder-blade (d) removed on the left side to show the ventral portions of the girdle); forelimb, with humerus (h), fused radius and ulna (r), wrist (1) and digits (g); pelvic girdle, the dorsal part of which (ilium, i) articulates with the sacrum (sacral vertebræ, sv); and hind-limb, with femur (f) articulating with the pelvic girdle, fused tibia and fibula (t), ankle with elongation of two bones, astragulus (a) and heelbone or calcaneum (c), and digits (k).

the vertebræ, which collectively form a stiff supporting rod for the attachment of the muscles of the trunk. There are nine vertebræ in the frog together with an elongated rod that represents a fusion of a number of the vertebræ of the posterior extremity. The latter is called the *urostyle*. The vertebræ consist of a main body or *centrum* and a more superficially situated arch (the *neural arch*) which invests the spinal cord (see Fig. 111, p. 266).

The movements of the limbs and jaws, etc., are not the only visible movements of which the frog is capable. If you open the abdomen of a freshly decapitated frog, you will see the heart rhythmically contracting and dilating, and on applying a series of electrical shocks to the outside of the stomach, it will be seen to become very noticeably constricted. It is by virtue of this power which the walls of the gut possess that the food is squeezed from one end of the digestive canal to the other in the normal course of events. The actual process of squeezing is not easily perceived in the frog, as its gut does not always contain much food material. But if we open the abdomen of a decapitated rabbit before it is cold we can see waves of writhing movement along the intestine. Galen (170 A.D.) understood that these movements of the gut and those of the uterus or womb, which assist in expelling the child from the body of the mother, are due to the fibrous walls of the alimentary and generative tracts, for he wrote :—

> the fact is that the stomach possesses two coats which certainly exist for some purpose ; they extend as far as the mouth . . . simple observation will show that these coats have their fibres in opposite directions. And, although *Erasistratus* did not attempt to say for what reason they are like this, I am going to do so. The outer coat has its fibres straight for traction. The inner coat has its fibres transverse for the purpose of peristalsis. . . .

The individual fibres of the muscular wall of the gut are

single cells (Fig. 12) without the well-defined transverse markings of striped muscle. They are spindle-shaped and each possesses a single nucleus. Heart muscle in the frog is somewhat intermediate in microscopic appearance between the " smooth " or " plain " muscle of the gut, and the striped muscles of the limbs. The individual fibres are single cells with single nuclei, but they have distinct transverse striations.

The properties of these three types of muscle in an animal like Man or the frog are different in several important respects while agreeing in their capacity to produce visible movements by shortening and thickening about their long and short axes respectively. It must be clearly appreciated that this power of contraction is an essential property of the muscle itself, in no wise dependent on the rest of the body, except in so far as the latter ordinarily supplies it with working materials. The frog's heart after removal from the body may be kept beating for days if perfused with a solution of salts like those in the blood.[1] Yet though independent of the body to this extent, on substituting a fluid similar in every respect except in the absence of calcium, it is brought to an almost immediate standstill, restarting in a few seconds if the original perfusion fluid is again introduced without too long delay. This is a material fact about the machinery of the heart which is as predictable and as definite as any experiment that we can carry out in the chemical laboratory. We see, therefore, that the heart muscle can be made the subject of experimental study as a separate piece of machinery. So also with a typical striped muscle such as the calf muscle (gastrocnemius) of the leg of the frog. For hours after removal from the body, if kept moist, it will contract if stimulated with electric shocks. The main difference between plain and

[1] $\frac{1}{8}$th molar solutions of NaCl, KCl, $CaCl_2$ in the proportions by volume 100:2.5:1.5 is a suitable medium. A little $NaHCO_3$ (about 0.02 %) should be added to keep it slightly alkaline.

striped muscle lies in the fact that striped muscle generally speaking does not contract unless a special stimulus is applied to it, whereas plain muscle, like cardiac muscle, has a spontaneous rhythmical activity. Furthermore striped muscle taken from the body is completely relaxed, whereas plain muscle is in a state of sustained partial contraction or *tone*.

(3) *Secretion*. One very characteristic feature of the

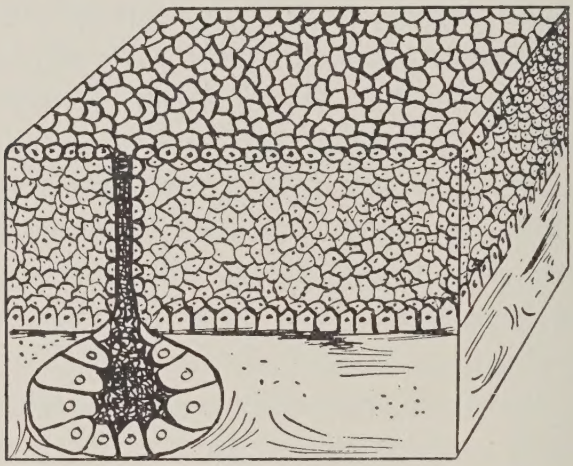

FIG. 14—SIMPLE GLAND FROM SKIN OF FROG OR TOAD SHOWING ALSO THE SUCCESSIVE LAYERS OF CELLS WHICH FORM THE OUTER SKIN OR EPIDERMIS

behaviour of amphibians (a group to which frogs and toads belong) is the readiness with which they emit a slimy material from their skins, especially if roughly handled or placed in water containing a little ether. The emission of this slime from the skin of the body is an illustration of the kind of response known as secretion. Glands are the parts of an organism which are concerned with the manufacture of what we call secretions; the spittle, phlegm, bile, sweat, etc., are instances of the latter. The simplest sort of glands are single cells, such as the mucous or slime cells scattered over the inside surface of the frog's intestine. Most glands are many-celled tubes or pockets of cubical cells with large

nuclei and often with conspicuous granules (Fig. 15). The term was originally applied only to those cases in which very large numbers of such tubes are packed together to form compact organs of visible dimensions like the liver, pancreas (sweet-bread), etc.

The skin glands of a frog or a toad are simple pits of large

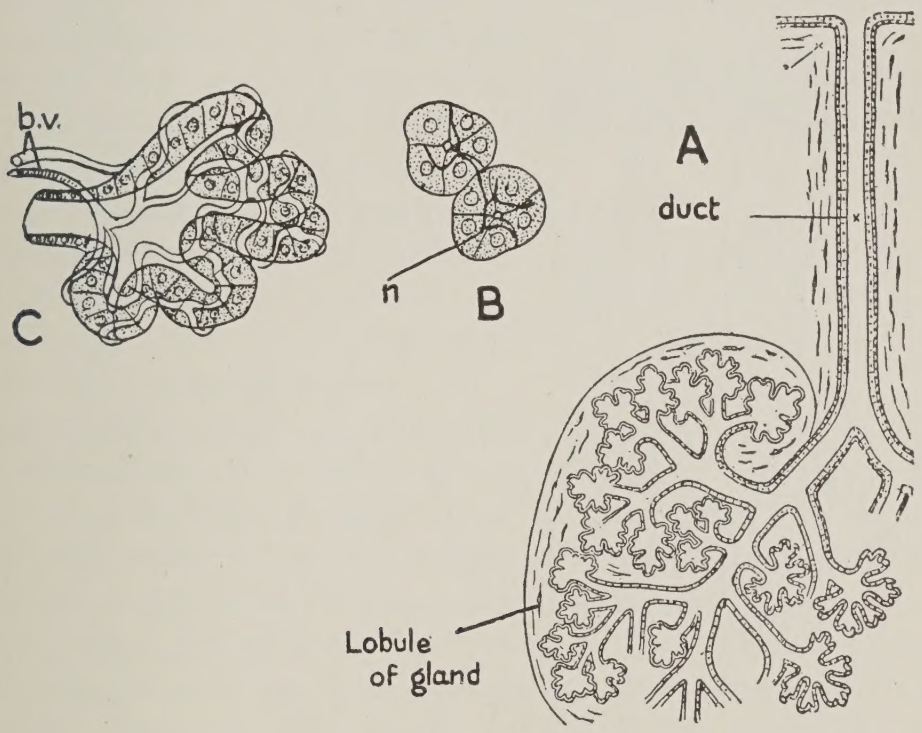

FIG. 15—GLANDS

A, Diagrammatic microscopic section through a lobule of a complex gland (Huxley). B and C, Microscopic sections through terminal secretory unit of the salivary gland of mammal, showing nerve (n) and bloodvessels (b.v.).

cells (Fig. 14), and the venomous secretion of the skin glands of some toads contains, in addition to mucous compounds which give to it a slimy character, a number of physiologically active substances. One of these is allied to the substance called adrenaline, secreted by the adrenal glands (Chapter V). The sweat glands of the human skin are relatively longer coiled tubes, but likewise unbranched. Their secretory product is a watery solution of salts. The

skin secretion of a toad is a response to mechanical stimulation of the surface of the body: possibly it aids the animal to escape from its enemies by making it more slippery to grasp. Sweat secretion on the other hand is a response to increased temperature, and its evaporation on the surface of the skin has the effect of cooling the animal. It is part of an elaborate arrangement which preserves the tissues of mammals at a remarkably constant temperature well above that of their surroundings in most circumstances. Only birds and mammals maintain a constant body temperature above that of the medium in which they live.

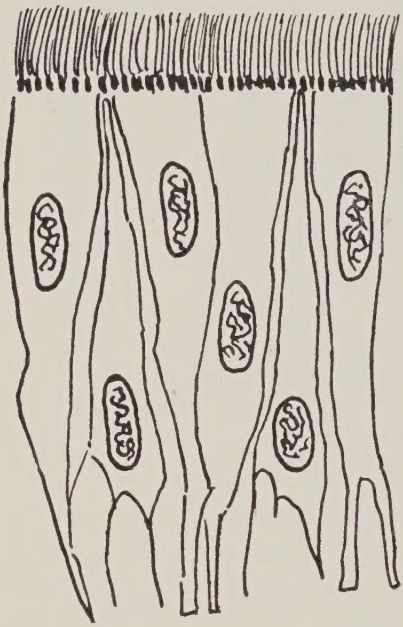

FIG. 16—CILIATED COLUMNAR EPITHELIUM FROM THE TRACHEA OF A RABBIT

(4) *Ciliary Motion.* A last form of response, which can easily be observed in the common frog, is that known as ciliary motion. We have already encountered it in the locomotion of Paramecium; but the reader may not have expected to meet with it again in a more complex animal. If we cut out a strip of the skin of the roof of the frog's mouth, and examine it under the microscope, we are able to see at the edges that the whole surface is covered with a layer of cells (Fig. 16) provided with fine vibratile filaments or cilia, like those which cover the body of Paramecium or Opalina. These cilia keep a definite movement of the slimy secretion of the mouth in the direction of the gullet. A few grains of charcoal sprinkled over the anterior end of the roof of the mouth of a frog killed by pithing, will move at a quite perceptible rate towards the throat. The

cilia of the same transverse row of cells beat together. The cilia of the row behind beat a short interval later so that the movement of all the cilia together resembles a field of corn blown by the wind. Ciliated epithelium occurs in man in the respiratory passages.

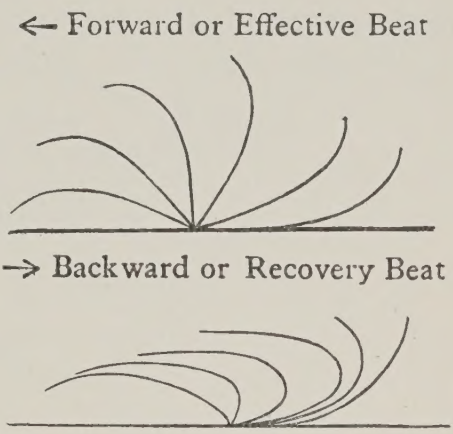

FIG. 17—DIAGRAM OF CILIARY MOTION

For the study of ciliary motion in the laboratory the common mussel (*Mytilus edulis*) affords a good illustration of a type of animal in which ciliary motion is a most important mode of response, since it is the agency by which the animal collects its food. The main part of the body in the mussel is situated along the mid-dorsal line below the hinge of the shell. (Fig. 18.) On either side there hangs down a fleshy film closely applied to the valve of the shell, and called the mantle lobe. The two mantle lobes enclose a cavity which, when the shell is partly open, communicates with the exterior only at the blunt end of the shell. This orifice is double, owing to the fact that the mantle lobes adhere at one point, so that there is an exhalant aperture separated by a thin sheet of tissue from an "inhalant" aperture lying below it. Through the inhalant orifice a current of water passes into the mantle cavity, at the opposite end of which is situated the mouth bounded by the fleshy labial palps. From the visceral mass hang down into the mantle cavity for the greater part of the long axis of the body a pair of so-called "gills." (Fig. 18.) These each consist of a pair of flat plates formed by the lateral approximation of a longitudinal row of filaments bent back to meet the body wall, so that each plate, or lamella,

encloses a chamber which communicates behind with the exterior by way of the exhalant aperture. A slow, continuous current of water enters through the inhalant orifice, strains through the filaments which make up the lamellæ

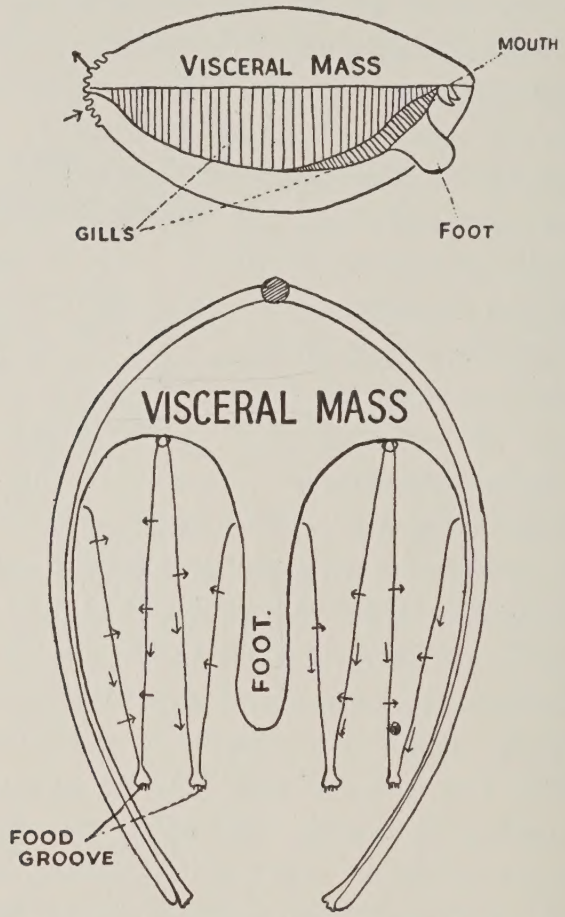

FIG. 18—DIAGRAM TO SHOW CILIARY CURRENTS IN THE GILL CHAMBER OF THE MUSSEL

Above—the animal as seen when one valve of the shell is removed ; below—transverse section through whole animal.

of the gills, passes backwards between the two halves of each lamella, and thence flows outwards by the exhalant aperture. It is maintained by the activity of cilia which line the sides of the filaments. (Fig. 19.) The whole apparatus is an animated filter ; it strains minute suspended particles out of the water-stream, sorts them, and conveys the nutritious

ones to the mouth. The gill-filaments secrete mucus. Entrapped in this slime, food particles are driven by the action of the cilia, which are also present on the exposed face of the gills, downwards to the lower margin of the lamella, which is grooved at its distal extremity. By ciliary

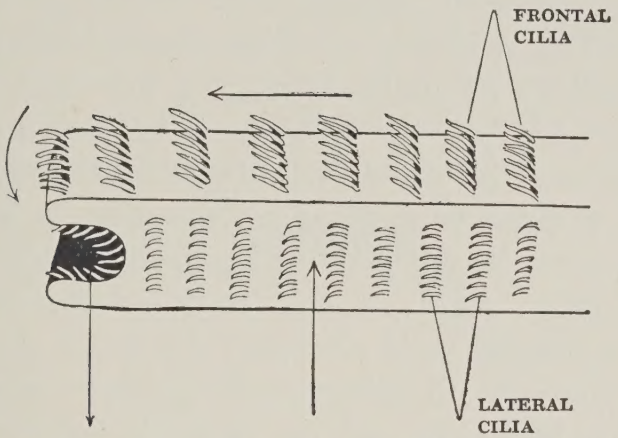

FIG. 19—GILL OF THE MUSSEL (diagrammatic)

Diagrammatic representation of a single filament to show the relation of different rows of cilia to the ciliary currents, which are indicated by arrows.

motion of the cells which line these grooves, a slimy stream of food particles is lashed forwards and on to the labial palps. These have a ciliated groove maintaining a current into the mouth. (Fig. 18.) The rest of the surface of the palps is covered with cilia, which drive coarse, unsuitable particles away.

II. The Receptor Organs

Having outlined the effector organs which are involved in the most striking responses of the frog we may now turn to a more detailed treatment of the receptor organs. At this stage we shall only deal with two of the more important receptors, namely, the Eye and the Ear. The normal movements of an animal are related to two chief types of stimuli, light and gravity. Everyone is familiar with the fact that many insects fly towards a candle. Blow-fly maggots if placed in a horizontal tube at right angles to

a window always move away from the direction whence the light comes. Examples of animal responses other than movement evoked by the agency of illumination have already been cited. The influence of gravity is less familiar but just as important. Gravity is a powerful factor in maintaining normal posture, and the chief one which determines the tendency of a cat, when thrown into the air, to orientate its limbs in such a way that it falls on all fours. The way in which gravity influences animal locomotion may be shown by observing whether animals placed on a slope tend to move upwards or downwards. In a few animals the influence of gravity is so important that they invariably react in one way or the other. But, generally speaking, it is necessary to eliminate other disturbances in order to observe the influence of gravity on an animal's behaviour, as for instance by observing its reactions in the dark, when the influence of light on its movements is excluded. Many small fresh-water shrimps, for instance, rise to the surface or sink to the bottom in the dark, some species moving away from and others in the direction of the pull of gravitation. One investigator who has studied the behaviour of young loggerhead turtles finds that they leave their nests and then crawl to the sea as the result of three responses which reinforce one another. First, other things being equal, they tend to move in the direction of the pull of gravity (positive geotropism); secondly, they move in the direction of the clearest field of illumination; thirdly, other things being equal, they move towards a blue source of light. The normal route of the young loggerhead turtle to the sea is a sloping beach with a clear horizon of blue. Given these responses to gravity and to the intensity and the colour of the light, one or all of the necessary stimuli will almost invariably be present to lead the animal to the sea in which it spends the rest of its life.

The ear in the frog and in ourselves is the organ by

which the influence of gravitation and the mechanical stimulus of sudden jerks are brought to bear upon the machinery of response. In ourselves, and to a much less extent in the frog, it is also a receptor organ for sound. Man differs from most other animals in the power of discriminating between sounds; in fact sounds are the stimuli that call forth a very large proportion of the responses of civilised life; for man alone has the power of speech well developed. It is the part played by the ear in determining an animal's position in space that is of most general

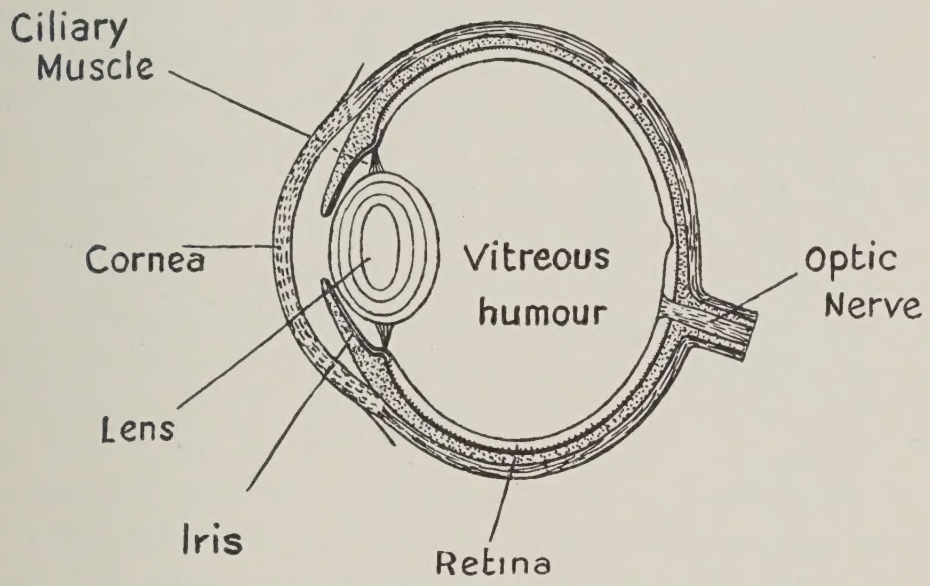

FIG. 20—THE VERTEBRATE EYE

importance to animal biology. Outside the great group of Vertebrates, of which the fish, the frog, the turtle, the bird and Man are types, it is doubtful whether any animals, except some insects, are susceptible to what we call sound stimuli, and it is only in birds and mammals, so far as we know at present, that this power is at all well developed. But almost all animals are influenced by the pull of gravity, just as almost all animals are influenced by light.

(1) *The Eye.* The eye is in its gross construction very much like an ordinary camera. It consists of a box or

capsule, a lens which focusses an image on the back of the box, and a layer of tissue, the *retina*, whose cells contain a substance chemically sensitive to light like the gelatin film of silver salt on the photographic plate or film. In front there is a transparent region of the tough and elsewhere opaque capsule. It is called the *cornea*. Behind, it is connected with the brain by the *optic nerve*. Among the receptive cells of the retina is a layer of pigment cells somewhat like those which occur in the skin of the frog, for they are contractile in the same sense. These cells also occur in the eye of Man, which is essentially like that of the frog, and they are the only remains of the pigmentary effector system of the frog or the chameleon which the writer or reader of this book possesses. The layer of black pigment cells may be compared to the coat of black paint with which the inside of the box of the camera is covered. Between the cornea and the transparent gelatinous bi-convex lens, there is a ring of circular muscles, the iris or pupil. The relaxation or contraction of the plain muscle of the pupil according to the intensity of the light increases or diminishes the size of the aperture, in a manner exactly analogous to the diaphragm of the camera. The wall of the box is partly muscular, so that the distance of the lens from the photographic plate or retina can be altered in much the same way as it is altered by the bellows of the camera. The lens is fixed in the box of the eye by tough tendinous tissue together with muscle fibres, called the ciliary muscle. In Man the

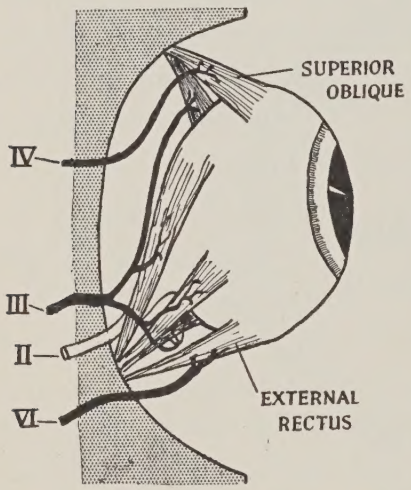

FIG. 21—THE VERTEBRATE EYE IN SITU

Showing associated muscles and their nerves.

focussing of the eye is performed by alteration of the shape of the lens by means of the ciliary muscles. The retina consists essentially of a layer of cells, the *rods* and *cones*, which contain the light-sensitive materials. Their diameter is about one ten-thousandth of an inch. The rods are like a very highly sensitive panchromatic plate, being affected by the intensity of light only. The cones are like a colour photographic plate, and they are not so sensitive as the rods, so that the colour, *i.e.* wave length of light reflected from different objects, is not so important in affecting an animal's behaviour in dim light as it is in broad daylight. Possibly this is one factor in determining the difference in dress and interior decoration that obtain in different countries. The rods and cones are in connection with a layer of nervous tissue which envelops them and is continuous with the optic nerve at the "blind spot."

The eye of the frog can be moved freely in its socket, like our own eye, by six muscles which will be referred to at a later stage. Very often the power to adjust the focus of the eye is inadequate to the requirements of civilised life. The eye may be too long, so that images from distant objects are focussed a little in front of the retina, or too short so that images from near objects come to a focus behind it. In the former case (myopia or short-sightedness) concave lenses, in the latter case (hypermetropia or long-sightedness) convex lenses of suitable curvature are used to effect the necessary adjustment. Another defect of the eye is encountered when the curvature of the cornea is not uniform. This peculiarity of the eye of many people is known as *astigmatism*, and can be compensated by lenses cut from the side of a cylinder, so placed in the spectacle frame that a suitable curvature is superposed in the plane which is relatively flatter.

(2) *The Ear.* The ear being, as we have already seen, a double structure, it will be best to describe its main features, and enquire later into the significance of its several parts,

and since the part of the ear concerned with sound is poorly developed in the frog, we shall first examine the structure of the human ear, and later call attention to the main points of difference between the two.

The ear of Man (Fig. 22) consists of the following parts: the external ear or pinna, only present in mammals and not in all mammals, and capable in some of being rotated to

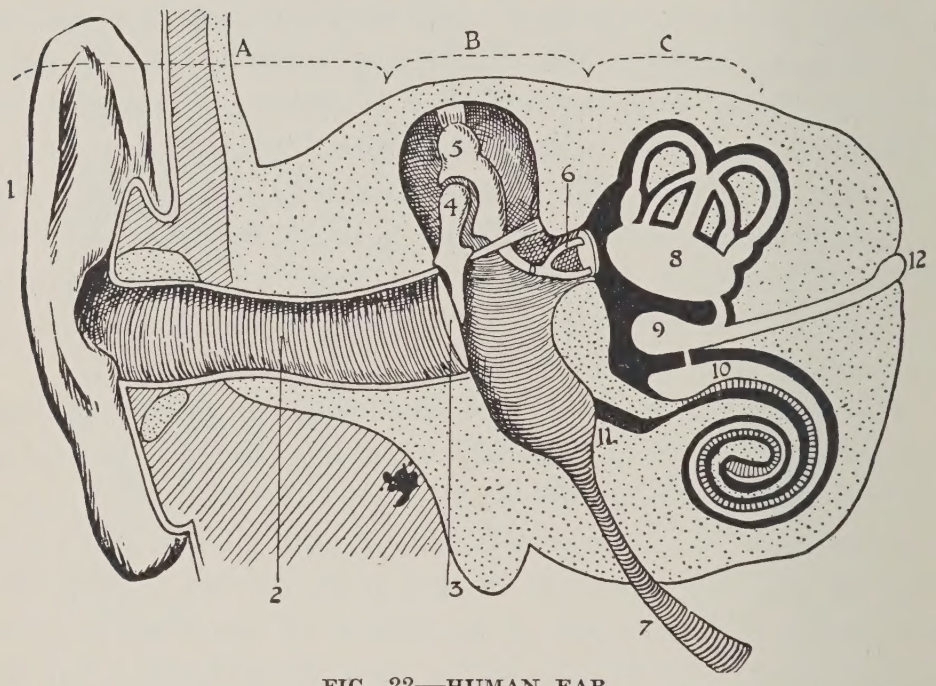

FIG. 22—HUMAN EAR

A, outer ear; B, middle ear; C, inner ear; 1, pinna; 2, external auditory meatus; 3, tympanum; 4, 5, 6, auditory ossicles; 7, eustachian tube; 8, utriculus; 9, sacculus; 10, cochlea.

collect sounds from different directions; a passage, the auditory meatus, that passes through a tunnel of bone ending blindly in an elastic membrane, the drum or tympanum; a cavity in the bone communicating with the back of the throat by the Eustachian tube; and finally a labyrinth of canals deeply embedded in the skull and communicating by a small window with the cavity behind the tympanum. This labyrinth encloses a complicated sac, which is the most essential part of the ear, the sac and the space between it

and its bony case being filled with a clear fluid. Across the space between the drum and the window of the bony labyrinth is a chain of three small bones, the auditory ossicles. These transmit vibrations from the former to the latter. The innermost sac consists of three portions. The uppermost or utriculus is continuous with three semi-circular canals at right angles to one another. Below it communicates with an elongated chamber, the sacculus, which leads into the third spirally coiled portion known as the cochlea. In the latter, which is specially concerned with

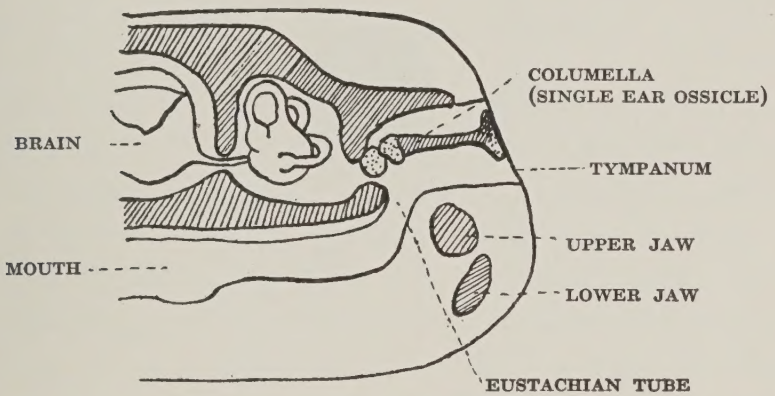

FIG. 23—DIAGRAMMATIC HALF SECTION THROUGH HEAD OF FROG
To show the auditory apparatus and labyrinthine organ.

sound, fine microscopic fibres joined by a membrane are stretched across its walls. The internal surfaces of the utriculus, semi-circular canals and sacculus bear patches of fine hairs in which nerve fibres end. In the cavities of the utriculus and sacculus are small lumps of calcium carbonate, known as *statoliths*.

Toads and frogs have a tympanum with a single auditory ossicle. But they lack a cochlea. It was not until the early part of the nineteenth century that receptivity of the ear to agencies other than sounds was first suspected, when Flourens (1824) investigated the effects of removing the semi-circular canals in pigeons. The inner ear of an

animal like the frog and the corresponding portions of our own ear are a rather elaborate form of a type of receptor organ that can be better understood in the simpler form in which it occurs—in jellyfishes, shrimps and some clams. Near the base of the feelers of the shrimp is a little sac containing a concretion of sand. The sand can be replaced by iron filings, and when this is done, the shrimp swims upside down, when a strong magnet is placed above it.

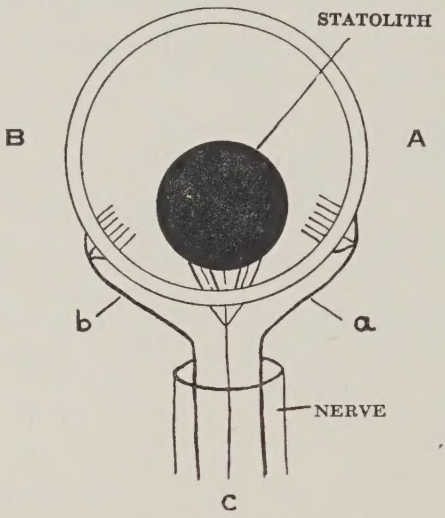

FIG. 24—DIAGRAMMATIC REPRESENTATION OF A STATOCYST OF A MOLLUSC OR SHRIMP WITH THREE NERVE FIBRES AND THREE GROUPS OF SENSITIVE CELLS

In the position shown the fibre (c) is stimulated. When the body rolls towards A, the statolith comes to lie on the sensitive hairs connected with (a). When the body tilts towards B, the statolith rolls on to the sensitive hairs connected with (b).

This shows that the position that the statolith occupies in the sac which contains it determines whether certain muscles are brought into play (Fig. 24). A shrimp which has had both its feelers removed will swim in a normal manner in daylight, but if illuminated from below in a dark room, it will swim on its back, whereas a normal shrimp will always swim so that its ventral surface is directed towards the pull of gravity. A shrimp with one feeler removed will swim normally in daytime. In the dark it will swim on one side. If both eyes and feelers are removed,

it loses all power to balance itself in water. If one eye and one feeler are removed, it swims perpetually in a spiral path. These experiments show clearly that the normal posture of swimming depends partly on light and partly on gravity. So long as both the receptors for either light or gravity are intact the influence of that stimulus is adequate to ensure the correct muscular responses. We shall go more thoroughly into this question, when we have seen how it is that the effect of the external stimulus on the receptor organ travels to the effector organ which carries out the appropriate response.

III. The Muscular Machine

We have now made a start in acquainting ourselves with the architecture of the animal body, by studying some of the parts which are most easily seen. Students who are pursuing their studies in chemistry and physics may wish to know if we have any idea how a muscle works. Those who are not doing so may defer the remainder of this chapter till a later stage. When Haller (1757) announced that a muscle, like the calf muscle of the frog's leg, isolated from the body, will continue to contract if suitably stimulated, a new horizon appeared. But it is only within the last century that much progress has been made towards the study of what actually happens in muscle contraction. Towards the end of the last century the following facts were known: (i) when muscle is repeatedly stimulated its power of contractility diminishes, but returns after a period of rest; (ii) when a muscle contracts heat is given off, the small rise in temperature being measurable by the sensitive electrical thermometer known as a thermopile; (iii) when a muscle becomes fatigued, lactic acid accumulates in it. More recently it has been shown that a muscle can contract in the complete absence of oxygen, but will only recover when oxygen is present. Oxygen, therefore, burns

away the lactic acid that accumulates in the muscle. Furthermore the appearance of a certain quantity of lactic acid in the muscle corresponds to the disappearance of a certain quantity of the muscle starch known as glycogen. Now if a muscle is stimulated in the absence of oxygen all the energy which is liberated can be measured as heat, and the amount of heat liberated corresponds exactly to the heat liberated in converting glycogen in the chemical laboratory into an amount of lactic acid equivalent to that which appears in the course of the contraction. From this we see that the muscle, like a motor-bicycle, is a chemical engine, only its energy is derived not from the oxidation of the glycogen but from its breakdown into lactic acid. We know that the work done in pushing out the piston of a motor-bicycle results from the fact that, when oxygen combines with petrol, an increase in volume takes place. We are not yet absolutely certain about how liberation of lactic acid causes a muscle fibre to shorten, but there are several ways in which it can well be imagined to take place. The chief constituents of muscle are substances like catgut (proteins) and fat. We know that addition of acid to a film of olive oil will cause the latter to contract, and we can bring about contraction of catgut fibres by the same procedure. The working of the muscle as a chemical engine is daily becoming more and more within our comprehension ; but an account of the experimental evidence for the conclusions stated above lies beyond the scope of this book.

Chapter III

THE MACHINERY OF CO-ORDINATION

WE have seen that the responses of an animal are carried out by definite structures (effector organs) localised in different regions of the body; that they are related to definite events in the external world; and that these events (or *stimuli*) are only capable of influencing the body through definite structures (receptor organs) not necessarily located in the same part of the body as that in which the appropriate response to their stimulation occurs. Hence arises the problem of *co-ordination:* what is the connecting link between receptor and effector? A disturbance occurs at one part of the body. Let us say, the image of a fly is focused on the retina of a frog: its tongue shoots out. A fly settles on the back of a cow: she whisks her tail and flicks it away. How does the disturbance travel to the tongue in one case, and to the tail in the other?

Let us now study a single unit of behaviour, some action that is the normal consequence of a particular stimulus. Such a sequence of events is called a *reflex*, and some examples of simple reflexes which can be easily studied in our own persons are given in the table below:—

Some Common Reflexes

Action	*Receptor*	*Effector*
Quickening of heart when its blood supply increases	Nerve-endings in right auricle	Heart muscle

Action	*Receptor*	*Effector*
Contraction of pupil in strong light	Retina	Plain muscle of iris
Secretion of saliva on smelling food	Olfactory organ	Salivary glands
Sneezing after pepper	Olfactory organ	Muscles of chest and diaphragm
Knee jerk	End organs in tendon	Extensor muscles of thigh

A reflex that is very easy to demonstrate in the frog is the withdrawal of the foot, when the toes are allowed to dip into water warmed to about the temperature of the human body. If we suspend a frog which has been pithed (*i.e.* the brain destroyed) with the legs hanging downwards and bring a beaker of water gently into position, so that the toes just dip into the water, we find that nothing happens if the water is at the temperature of the room; but the leg is pulled up if the water is previously warmed to about 40° C. If we time the interval between the immersion of the toes and the withdrawal of the limb, we find that it is a matter of seconds. Something has been happening during those seconds. What and where?

The chief means of transmission of the disturbances set up in the receptor organs to the effector organs that carry out the responses which ensue is the *nervous system*. [It is an instructive experiment to hang up five decapitated frogs in the manner indicated above, snipping away in each

case the bone known as the urostyle to expose two groups of shining white cylindrical trunks which are then seen to pass from the backbone downwards to the muscles of the legs. By a very simple procedure we may now learn what is the path by which the disturbance set up in the temperature receptors of the skin of the toes travels to the muscles of the thigh. In one frog the white trunks (*sciatic nerves*) of both sides are left intact. In a second the sciatic nerve of the right side is cut. In a third frog the sciatic nerve of the left side is cut. In a fourth frog the sciatic nerves of both sides are cut. And in a fifth frog neither are cut, but a wire is passed down the canal of the backbone to destroy the marrow or *spinal cord.* Having done this we may try the effect of letting the toes of both feet dip into warm water. In the first case both legs are withdrawn. In the second case the left leg is withdrawn. In the third case the right leg is withdrawn. In the fourth case and also in the fifth case neither leg is withdrawn. From this we conclude that the *something* which is happening between the immersion of the toes and the withdrawal of the foot travels by a definite road, namely along the sciatic nerve; and further that it travels first up to the spinal cord and then down to the leg muscles. This something we call the *nervous impulse.*

The Nervous Impulse. Propagation of a disturbance from the receptor to the effector is a physical property of the kind of matter that we call nerve. The nervous impulse is a physical event. It has space, time and mass relations. The first we have shown by experiment. As regards the second, the actual rate at which the nerve impulse travels can be determined exactly. This was first done by Helmholtz, in 1851, six years after Muller had stated that to measure its velocity of propagation was theoretically impossible. The method employed is very simple in principle, though special apparatus is necessary (Figs. 25 and 26).

First the sciatic nerve is cut out, together with the gastrocnemius (calf) muscle which pulls up the leg in the previous experiment. A certain time elapses between the application of an electrical stimulus to a nerve and the onset of contraction in the muscle connected with it. When the stimulus is applied at two successive points along the length of the nerve, it is found that the delay is less in the case of a stimulus applied to a point nearer the nerve-muscle junction. Dividing the distance between the two points on the

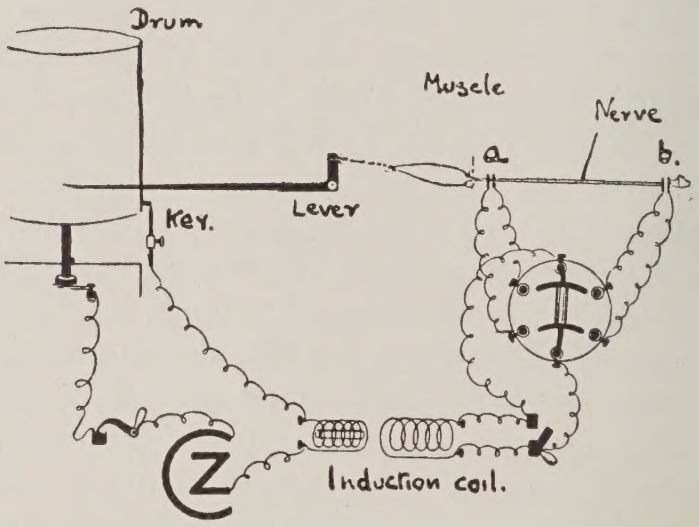

FIG. 25—APPARATUS FOR DETERMINING VELOCITY OF THE NERVOUS IMPULSE

nerve by the difference in the delay, we obtain the rate at which the nervous impulse travels. In the frog the rate is about eighty miles an hour at the temperature to which it is normally exposed.

What is it that travels along the nerve at this rate? Reactions of dead matter are retarded or quickened by change of temperature. By carrying out experiments such as the foregoing it can be easily shown that the velocity of the nervous impulse also varies in a definite way with change of temperature. The stimulation of nerve is accom-

panied by a measurable increase in formation of carbon dioxide. In other words the nervous impulse is associated with the transformation of a measurable quantity of matter. It is of interest to note that the chemical changes that occur along the length of a nerve, when the nervous impulse is said to traverse it, give rise to measurable electrical phenomena which can be measured by a suitable instrument—the Einthoven String Galvanometer.

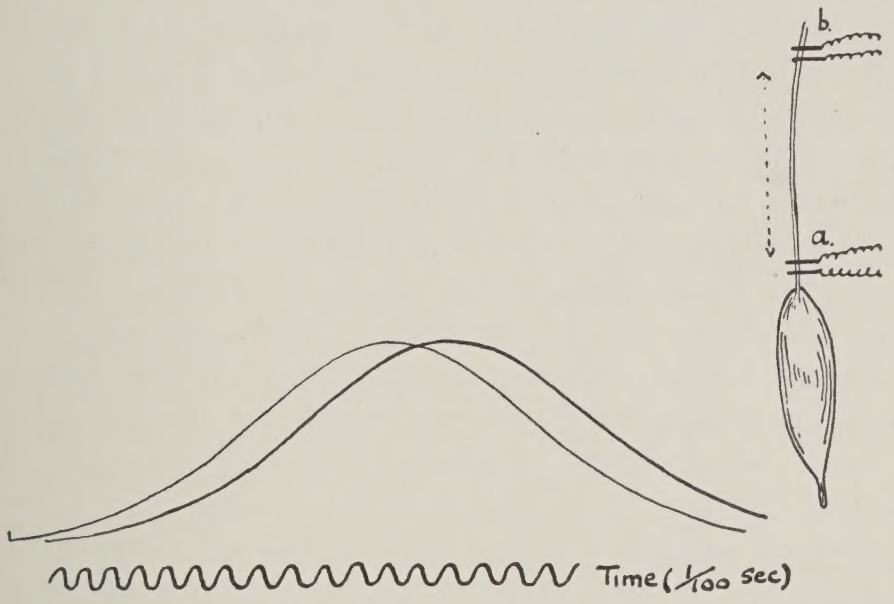

FIG. 26—MUSCLE RECORD, SHOWING DELAY ON CONTRACTION WHEN STIMULATED AT DIFFERENT POINTS (A AND B) ALONG THE LENGTH OF THE ATTACHED NERVE

A clear appreciation of the significance of the nervous system in the economy of the animal body came late in history. Galen, the foremost physician of antiquity, had no clear idea of the way in which disturbances are transmitted. A new understanding began in the year 1543, when Vesalius published his celebrated *Fabrica Humani Corporis*. Vesalius " dared not only to show how often Galen was wrong, but to insist that when Galen was right he was to be followed,

not because he said it, but because what he said was in accordance with what everyone who took the pains to inquire could assure himself to be the real state of things."[1] In the chapter on vivisections in his great book, Vesalius showed that by cutting or ligaturing one nerve or another the action of this or that muscle can be abolished, and that by removing the ligature the action of the muscle is restored, thus proving that the propagation of disturbances through the body is effected through the agency of the nerves. He also showed that transection of the spinal cord prevents the propagation of stimuli from the region above it to the muscles supplied by nerves emerging from the central nervous system below the section. It is customary to distinguish the brain and spinal cord of the frog as the *central nervous system* (commonly written C.N.S.) in contradistinction to the other nerve cords which connect it with the receptor and effector organs of the body. It was not until 1751 that the central nervous system was clearly recognised to be the turning point in the road which the nervous impulse travels, when Whytt showed by experiments on frogs that destruction of the spinal cord abolishes reflex actions. Before we can get a deeper insight into the adventures of the nervous impulse as it travels first towards the central nervous system, and thence outwards to the muscles, glands, etc., we must examine the microscopic structure of nerves.

Structure of the Nervous System. On teasing a nerve like the sciatic nerve of the frog, it is found to be made up of innumerable cylindrical fibres each of microscopic thickness, and each surrounded by a minute sheath of fatty material. On tracing these fibres back to the spinal cord it is eventually found that they are simply attenuated processes of branching cells. Some of them originate from branching cells in the grey matter or core of the spinal cord, where their

[1] Foster. *History of Physiology.*

finer branches are closely connected with the terminal branches of other nerve cells or *neurones*, as they are technically called. Branching cells of this type also occur in the central nervous system itself: their fibres run up and down the outer rind or white matter of the spinal cord, carrying nervous impulses from one level to another. Others of the fibres of a mixed nerve like the sciatic nerve of the frog, *i.e.* a nerve carrying impulses both to and from the cord, do not have their cell bodies within the spinal cord, but in swellings known as the dorsal root ganglia, situated near where the nerve is joined to the cord. We shall have more to say about these ganglia later; it suffices for the present to note that the term ganglion is used for any part of the nervous system in which the cell bodies of nerve fibres are congregated. The cells of the dorsal ganglia send branches into the spinal cord, where they arborise around the cell bodies found in the grey matter. A single nerve fibre, with its sheath, in the frog or Man, is not more than a hundredth of a millimetre in thickness, though in ourselves it may be as much as a yard in length.

The experiment cited earlier indicates that a nerve like the sciatic nerve of the frog is a bundle of fibres, some carrying nervous impulses in one direction, others capable of transmitting nervous impulses from the cord to the effector organs. We speak of the two kinds of fibres as *afferent* and *efferent* respectively, because any particular fibre is of one or the other type, the two being visibly different. On tracing any nerve back to the spinal cord, we find that it is connected with it by two separate trunks, the dorsal and ventral roots. The former has a thick swelling called a ganglion, in which are found, in addition to fibres, cells from which fibres pass in both directions, towards and away from the cord. If we cut a spinal nerve at its peripheral end, we can, by stimulating the nerve electrically on the central side of the cut, obtain characteristic reflexes by setting up

impulses in the afferent fibres. On cutting the dorsal root these reflexes will not be obtained, thus showing that all the afferent impulses pass into the cord by the fibres whose cells are located in the dorsal root ganglion. If, leaving the dorsal root of the nerve which we have isolated intact, we cut all other dorsal roots of the remaining spinal nerves, we do not find that the reflex activities which follow after

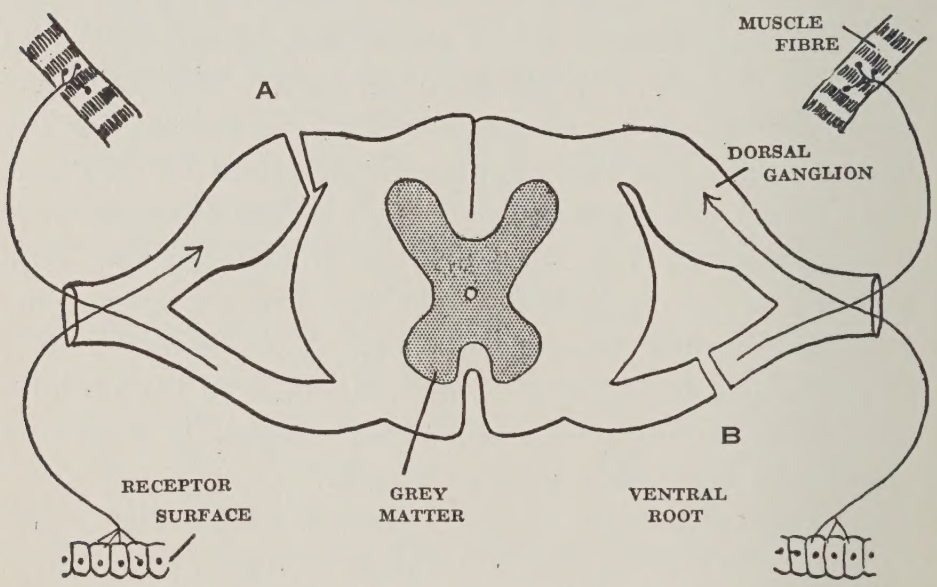

FIG. 27—DIAGRAM TO ILLUSTRATE MÜLLER'S EXPERIMENT

Dorsal root cut at A. Ventral root cut at B. The large circle in the centre represents the spinal cord cut across.

stimulating the cut nerve are interfered with at all. This indicates that all the efferent fibres leave the cord by the ventral root. The separate connections of the afferent and efferent neurones to the C.N.S. were fully elucidated by Johannes Muller (1834) who severed all the dorsal roots on one side of the body of a frog, and all the ventral or motor roots on the other side (Fig. 27). Such an animal shows complete indifference to stimuli on the side on which the dorsal roots are cut and complete inability to respond by

active movement on the opposite side, but stimuli applied to the side on which the dorsal roots are intact will evoke response on the side whose motor roots are intact. Magendie (1812) had found the same rule to hold good for the dog, Panniza (1834) established its truth in the bird, and later workers, including Stannius, applied it successfully in experiments on fishes.[1]

Actually it is not possible by microscopic section or by teasing a mixed nerve to infer that all the fibres of a dorsal root have their cell bodies in the dorsal root ganglion or that all the fibres in the ventral root have their cell bodies

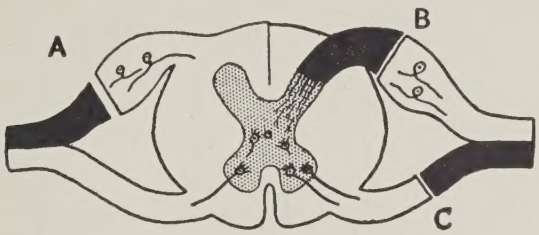

FIG. 28—DIAGRAM TO ILLUSTRATE EFFECT OF SECTION IN NERVE DEGENERATION

Degenerated regions black. A, dorsal root cut on peripheral side of ganglion; the afferent fibres to the left have degenerated. B, dorsal root cut on central side of ganglion; the ends of the afferent fibres carrying impulses into the grey matter of the spinal cord have degenerated. C, ventral root cut; the efferent fibres to the right have degenerated.

in the grey matter of the cord. The microscope enables us to see that fibres from the cells in the dorsal ganglia pass a certain distance towards and away from the C.N.S. and that the fibres of the cells in the grey matter pass out into the ventral root. We can only trace them by direct observation for a small fraction of their course, and then lose track of them. But experiment here comes to our aid. If we cut through a mixed spinal nerve, keeping the animal alive, we find that after a few weeks all the fibres

[1] The presence of separate afferent and efferent roots is a peculiarity of the nerves of vertebrates (Fishes, Amphibia, Reptiles, Birds and Mammals).

on the side of the nerve remote from the C.N.S. undergo degenerative changes. If we cut the dorsal root on the central side of the ganglion all the fibres on the central side of the cut degenerate. If we cut it on the peripheral side of the ganglion all the fibres on the peripheral side of the cut degenerate. If we cut the ventral root we find that degeneration occurs only on the side remote from the central nervous

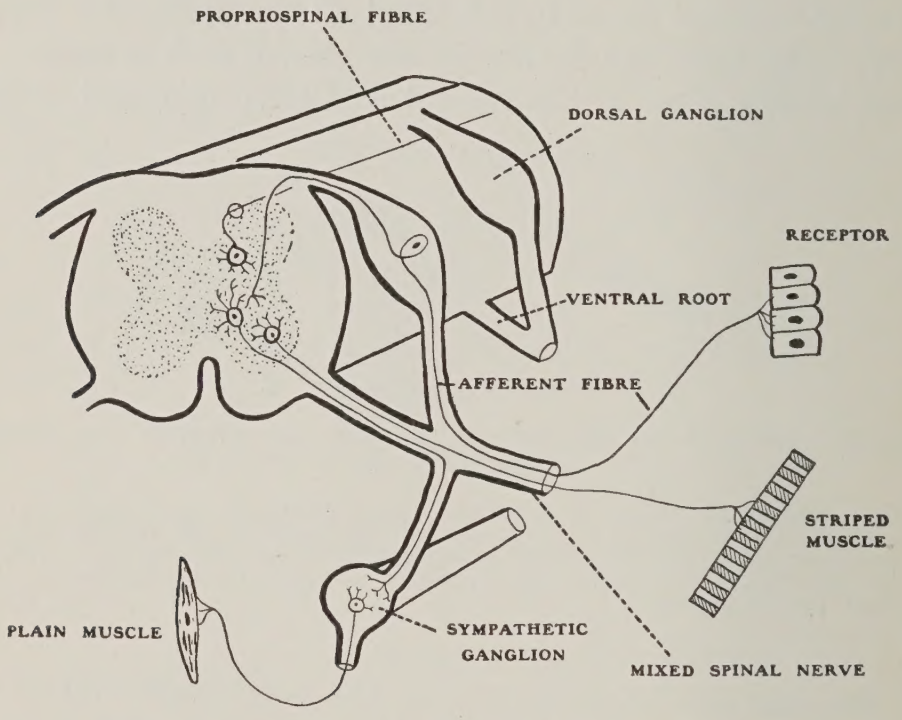

FIG. 29—DIAGRAM OF THE REFLEX ARC

system. We thus see that if cell bodies occur in any tract of nerve tissue, the fibres degenerate on the side of section remote from the seat of the cell bodies, or in other words that a fibre not connected with its cell body undergoes degeneration. Thus by applying the method of degenerative section combined with direct observation of microscopic preparations we are able to reconstruct the nerve paths involved in a reflex (Fig. 28).

FIG. 30—EFFECT OF FARADIC STIMULATION OF THE ROOF OF THE MOUTH IN THE CAPE CHAMELEON WHEN THE SPINAL CORD IS SEVERED AT C.

So the simplest possible path of a reflex (reflex arc) is by way of a fibre having its cell in the dorsal ganglion into the cord, across the thin membrane (or *synapse*) separating the ultimate branches of such a fibre in the grey matter from the branched cell body of an efferent neurone, whose fibre passes out by the ventral root. Then the latter fibre is bound up with other fibres, carrying impulses inwards or outwards, in a nerve trunk (Fig. 29). This, however, is a very simple type of nerve path involved in reflex action. There are large numbers of neurones whose whole length is confined to the C.N.S., running up or down, carrying impulses from afferent neurones at one level to efferent neurones at another. There are two great meeting places within the C.N.S., for the neurones which run forwards to the head and backwards to the posterior extremity, namely the grey matter of the two portions of the brain known as the cerebrum and cerebellum. When the brain is destroyed these paths are eliminated: and partly for this reason, partly for others which will be referred to later, the behaviour of the pithed frog is much simpler, and therefore more suitable for the study of reflex action than that of the normal animal.

The existence of nerve tracts running up and down the spinal cord can be demonstrated in a very simple way. When a dark chameleon, *i.e.* a chameleon (Fig. 30) which has been kept a few minutes in bright light in a cool room, is stimulated by an alternating current from a shocking coil by electrodes (two pins connected by wires to the terminals serve this purpose) applied either to the roof of the mouth or to the anal orifice, the animal becomes extremely pale after about a minute. If now the spinal cord is cut with a pair of dissecting scissors about the level of the eighth vertebra, it is found that on stimulating the mouth, the skin becomes pale only in the half of the body in front of the cut, whereas on stimulating the cloaca the body becomes

pale only on the posterior side of the cut. The nerve fibres that supply the striped muscles of the limbs,

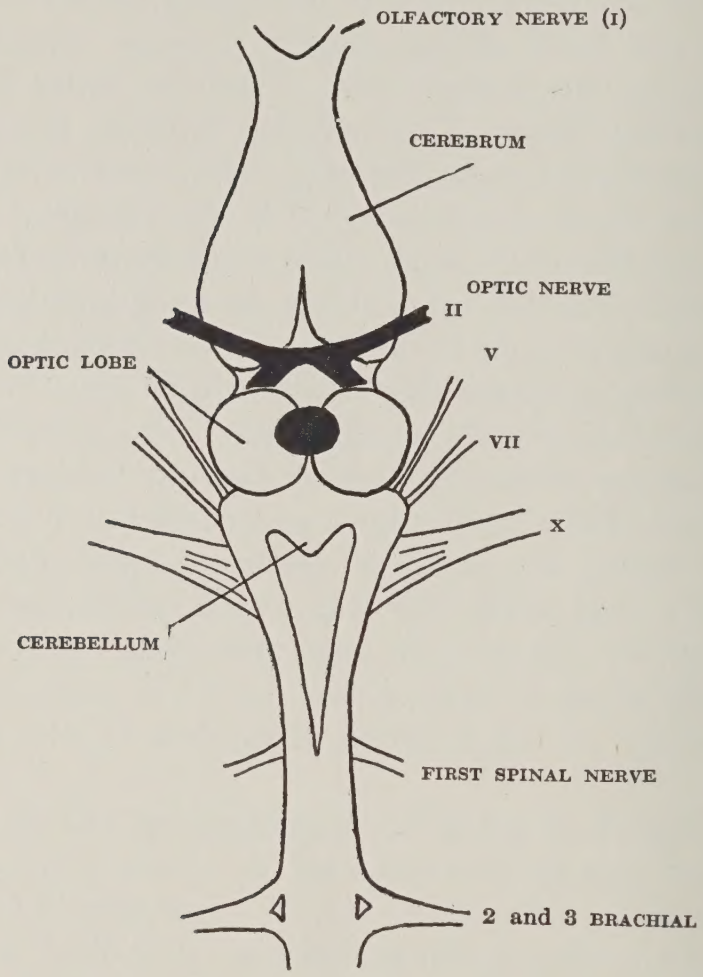

FIG. 31—BRAIN OF FROG

The optic nerves (II) and pituitary body, represented in black, lie on the ventral side of the brain. The rest of the picture is a dorsal view.

etc., have their cell bodies in the grey matter of the cord.

The nerve supply of the smooth muscles, of the muscles of the heart and of the glands (as well as that of the pigment cells of the chameleon or fish) is somewhat different. Con-

nected with each pair of spinal nerves by fine trunks known as *rami communicantes* are certain swellings of nervous

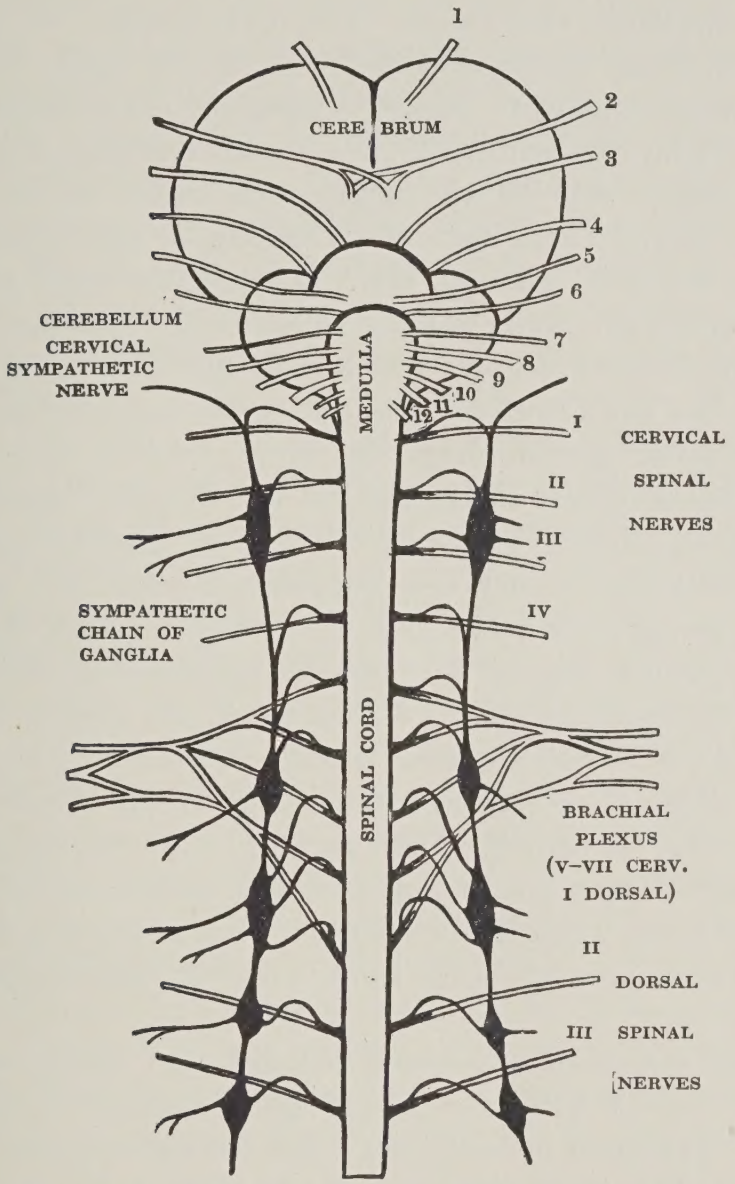

FIG. 32—DIAGRAMMATIC REPRESENTATION OF THE CENTRAL NERVOUS SYSTEM OF MAN

tissue containing nerve cells as well as fibres and therefore called ganglia, or usually *sympathetic ganglia.* When the

rami or ganglia themselves are stimulated by an electrical current from a shocking coil, characteristic responses of the musculature of the gut, walls of the arteries and generative passages, glands, etc., occur. When the ganglia are painted with the drug nicotine, stimulation of the rami does not evoke these responses. Since painting the nerves themselves does not prevent their ability to transmit impulses, it appears that nicotine acts on the nerve cells which occur in the ganglia only. These nerve cells belong to neurones which supply the gut, glands, etc. They differ from efferent neurones which supply striped muscle *via* the spinal nerves and from the nerve fibres which pass out of the cord to the ganglia *via* the rami communicantes in that they have no fatty sheath surrounding the fibre itself. The nerve fibres that originate in the ganglia are therefore called non-medullated fibres. From the fact that nicotine prevents the conduction of nervous impulses beyond the ganglia by paralysing their nerve cells, it is concluded that the plain muscle, glands, etc., of the body are not directly innervated by the fibres whose cells are situated in the grey matter of the cord; but that impulses leaving the C.N.S. for effector organs other than striped muscle pass in the ganglia to a second relay of neurones. In fact the sympathetic ganglia are distributive centres which permit impulses arriving from the cord along a single fibre to set up relay impulses in large numbers of non-medullated fibres going to different destinations.

In the region of the spinal column—the spinal cord—a pair of nerves with motor and ganglionated roots arises between each pair of vertebræ. But the main nerves to the limbs, such as the sciatic nerve, are formed by the union of several of these. The anterior end of the C.N.S. is considerably swollen and enclosed within the skull. From this region, the brain (Fig. 31), there emerge both in the frog and ourselves ten pairs of nerves called *cranial*

nerves.[1] These nerves—especially those of the anterior end of the brain—are not built on the same plan as the spinal nerves. The same nerve does not always contain both afferent neurones and efferent neurones supplying striped muscle. They have various names, but are conventionally denoted more briefly by roman numerals.

Starting from the most anterior pair they are :— I. The Olfactory nerves from the nasal receptor surface : purely afferent. II. The Optic nerves from the retina : purely afferent. III, IV and VI are efferent nerves supplying the striped muscles which move the eye in its socket. There are in the frog and in man six of these in each eye socket or orbit. They are called the anterior, posterior, dorsal, and ventral rectus muscles, and the dorsal and ventral oblique muscles (Fig. 21). The anterior (internal) rectus, the dorsal (superior) rectus and the ventral (inferior) rectus and oblique muscles are innervated by III. The posterior or external rectus is innervated by VI and the superior or dorsal oblique by IV ; VIII is a purely afferent nerve with two divisions from the two separate portions (utricular and cochlear) of the ear. The remaining cranial nerves, V, VII, IX and X contain afferent neurones—V from the skin of the face and in the human subject the pulp cavities of the teeth, VII from the skin of the face and in the human being the receptive surface of the tongue, IX and X from the respiratory and digestive tracts. But they also carry medullated fibres with cells in the brain itself. Some of these go to the muscles of the face and throat. Others end in connection with short non-medullated neurones in the musculature of the gut or heart. Stimulation of the Xth or Vagus nerve of the frog, as in our nearer allies (*e.g.* rabbit or dog), always results in slowing and enfeebling of the heart beat. This nerve exerts a restraining influence on the rhythm of the heart.

1 Two additional nerves of Man (and other Mammals)—in reality typical spinal nerves—are incorporated in the skull cavity.

It is an interesting fact that the stimulation of the vagus nerve always has the opposite effect to the stimulation of the spinal sympathetic nerve supply of any particular effector. Thus stimulation of the sympathetic nerve produces relaxation, stimulation of the vagus contraction, of the muscular wall of the gut. Stimulation of the sympathetic nerves to the heart increases the rate and power of its beat.

The brain itself is that part of the C.N.S. which receives impulses from the most important receptor organs—the eye, ear and olfactory membranes, transmitting them by the descending neurones within the C.N.S. to the efferent neurones that arise from the cord at different levels. For anatomical description it is—somewhat arbitrarily—divided into three regions : the *fore, mid* and *hind* brain. The fore-brain consists of two parts, a more anterior portion, the dorsal aspect of which is called the *cerebral hemispheres*, and a more posterior portion which is narrower (the *thalamencephalon*) and bears two interesting glandular structures on its roof and floor. The former is the *pineal* body which in some lizards has an eye-like structure. Whether it is of any importance to the frog we do not know—probably it is not. The second is called the *pituitary* gland. Of this organ we shall have more to say later. The roof of the mid-brain is defined by two globular lobes, the so-called *optic lobes*. The hind-brain is poorly developed in the frog. Its roof in the human being is called the *cerebellum*. The first two pairs of cranial nerves arise from the fore-brain, III arises from the floor of the mid-brain, IV emerges dorsally between the mid and the hind-brain, and V—X arise from the floor of the hind-brain. A frog in which the brain has been destroyed may be kept alive indefinitely ; and its behaviour is very much simpler and therefore more easy to predict after careful study. It is no longer subject to the very varied stimuli of ever-changing images from the retina, and of

smells or noises in its vicinity. The interplay of all these of itself makes the behaviour of the intact frog a much more complicated affair.

The Study of Behaviour. When the influence of one group of stimuli, *e.g.* light, predominates over all others, it is possible to see how simple reflexes like the ones we can study in the pithed frog determine the behaviour of an animal. Thus it is proverbial that certain insects move towards the light. A generation ago we should have said they move towards the light because they like the light. This tells us nothing. It is not really very different from the habit of mind which made the alchemist speak of " spirits " of nitre, " spirits " of salt, etc., attributing to personal agencies all the properties of dead matter as the savage peopled his universe with unseen beings. The matter of fact way of looking at things which we call science does not view the insect in this way. For scientific treatment the insect is a physical object. Experiment shows that when light falls on one eye of the insect, the muscles of that side contract more powerfully than those on the other side. When an insect is moving in a direction parallel to the rays of light both its eyes are equally illuminated. As soon as it turns to the right or left one eye will be more powerfully illuminated than the other. With increase of the contraction of the muscles that side of the body is bent round, till both eyes are again equally illuminated, when the action of the muscles of the body is again balanced. This is a mechanical necessity of reflex action; and with such an understanding we can predict many things about an insect's behaviour that could not be known otherwise. For instance,

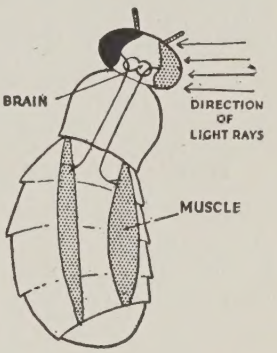

FIG. 33—DIAGRAM TO ILLUSTRATE MOVEMENT OF INSECT TOWARDS THE LIGHT

if we blacken one eye, we should expect that the muscles of the body on that side in the case of an insect which moves towards the light would remain permanently more relaxed than those of the opposite side, so that the animal is compelled to move round in a circle with the blackened eye on the outside (Fig. 33). But there are insects, such as fully grown blow-fly larvæ, in which the state of affairs is reversed, and which normally move away from the light ; these would move in circles with the blackened eye towards the inside. Both these results can be verified by performing the experiment, which was first carried out by Jacques Loeb (1889).

With the knowledge that we now have we can form a clearer picture of the way in which such a receptor as the statocyst of a shrimp, or its more complicated counterpart the membranous labyrinth or inner ear of the frog, performs its rôle in the maintenance of normal posture. The inner wall of the statocyst of the shrimp is covered with cells provided with fine hairs projecting into its cavity (Fig. 24). These cells are connected with the ends of separate nerve fibres. When the body changes its position, the statocyst, owing to the pull of gravity, rolls from one set of hairs to another. If different nerve fibres of the statocyst belong to reflex arcs involving different sets of muscles, one or another set of muscles will be brought into play by the mechanical stimulus of the statolith resting on one or another set of hairs (Fig. 24). This roughly speaking is the mechanism underlying the fact that a cat falls on all fours.

In the spinal cord or brain of an animal like the frog (or the writer of this book) the neurones do not lie in isolated reflex arcs, but each is connected by its ramifying branches to a number of others. The occurrence of any reflex implies that impulses pass across the junction between two particular neurones more readily than across the junction of the same neurones and all others. That is to say,

reflex action is a physical property of the *junctions* between nerve endings in the C.N.S. Seeing that the animal is subjected to innumerable stimuli simultaneously in normal life, its behaviour would be quite chaotic were it not for an important feature of reflex activity. Suppose the stimulation of a receptor A produces relaxation and of B produces contraction of a certain muscle which in ordinary conditions is in the state of steady incomplete relaxation known as "*tone*." When A and B are stimulated simultaneously, either A holds the field alone or B, that is to say the response is exclusively characteristic of stimulating either A or B alone. In such a case both reflexes have common efferent connections called by Professor Sherrington a "final common path." Now in the C.N.S. the number of fibres running up and down are by no means infinite in number, and enormous numbers of reflexes share common paths in the cord. The fact that one group of receptors can use a common path to the exclusion of any antagonistic reflex system renders the behaviour of the animal more stable and definite than it would otherwise be.

The Nature of Conscious Behaviour. The relatively simple behaviour of the pithed frog as compared with that of the intact animal is not exclusively due to the fact that the influence of the great sense organs of the head is eliminated, nor to the fact that many of the possible ascending nerve paths which converge on descending ones at a higher level are cut across. To some extent—far less than the reader or writer of this book—the frog can, in the language of everyday life, *learn*. That is to say, a stimulus that has been repeated a large number of times can under certain conditions become the signal for a response which it did not formerly call forth. These conditions can now be studied by experiment and to a very large extent described in the language of science.

The ability to build up new reflexes under definitely ascertainable conditions is a physical property of the fore brain or cerebrum. Extraordinary progress in defining the conditions under which new reflex systems are built up has been made during the last fifteen years by the Russian physiologists of Pavlov's school. This is a very revolutionary development of modern science, because it brings within the realm of scientific treatment a body of experiences which have hitherto been the province of metaphysics. It is the essence of scientific method that it deals only with relations that are the result of external observation; that it aims at expressing these relations in quantitative terms, and that it employs no assumptions that can be eliminated without affecting the verifiability of its conclusions. In other words science might be defined as measurement in the service of prophecy. The fact that it is now possible to study the machinery by which the effect of previous stimuli modify the behaviour of an animal at any given moment brings within the scope of scientific treatment things which have hitherto been ascribed to non-measurable agencies such as " memory," " consciousness," " sensation," and the like.

The capacity to learn is one of a number of characteristics of behaviour which distinguish the intact frog from the brainless frog. These characteristics correspond to what are called in traditional language " conscious behaviour." It has been customary in the past to assume that the behaviour of an animal can be treated of under two headings, " reflex " activity which we have referred to briefly above and " voluntary activity " or " conscious behaviour." The former alone has been regarded as the proper domain of the biologist. It has been usual to regard the latter as the province of moral philosophy. The success of Pavlov's researches show that the method of science is capable of dealing with conscious behaviour. But we cannot consider

his work without going more fully into the details of spinal reflex activity than the space at our disposal permits. The reader must refer to a more advanced book (see Appendix I) for an account of the way in which it has been done.

Chapter IV

THE SOURCES OF ENERGY OF THE ANIMAL BODY

WHEN any change occurs in the world around us, we say that work has been done or that energy has been transformed. A living creature is always changing in one way or another. We have studied some of the characteristic forms of change which it displays and the sequence of events which constitute that extraordinary pattern of change which we call an animal's behaviour. So now we have to ask, what is the mechanism of all this transformation of energy which is called life? This is perhaps the deepest and most fascinating of all problems, and it is not an easy one to discuss, unless we know a good deal about the way in which changes take place in the world of dead matter. The student who is genuinely interested in animal life will not shirk his studies in chemistry and physics, or even in mathematics, which at first sight seem remote from the problems of animal life. A knowledge of the machinery of physical change provides the key to the most mysterious of all changes of which we have experience.

Energy of the living machine. The fundamental Law of Energy is the Principle of Conservation. A fixed quantity of heat is always equivalent to a given amount of mechanical work in any machine. When a machine is generating both heat and movement we can express the total energy it is giving out either in purely mechanical units or in heat units (calories). In the case of the motor-bicycle it is found that for a given amount of petrol consumed, the total energy (heat

and movement) resulting is the same : the difference between economical running of an engine and uneconomical lies in whether the ratio of mechanical to thermal production is higher or lower. If we run with the brakes partly on, the same amount of energy is liberated by the explosion : the difference in speed is made up by the heating of the brake blocks, rim of the wheel, etc. When the petrol of a motor-bicycle gives out, the machine stops. Living matter, like a motor-bicycle, is constantly doing work, often like the motor-bicycle in the form of movement from one place to another or of the emission of startling noises. From time to time the living machine has to be fed like the petrol tank of the motor-bicycle. Actually no living machines feed like motor-bicycles on petrol. But the energy of the living machine depends on the chemical materials with which it is supplied as truly as the energy of the motor-bicycle depends upon the petrol, benzene, paraffin or other hydrocarbon with which it is supplied.

Living creatures, like a frog or a human being, are all subject to the same inexorable restriction. Their principal activities belong to the same two categories as those of the motor-bicycle. At the moment of writing the author is raising the temperature of the room with the heat of his body, while doing mechanical work in thumping upon a typewriter. While the motor-bicycle is working, petrol is being burnt up. Motor-bicycles breathe in oxygen and breathe out carbon dioxide, just as they feed on petrol. If we give a motor-bicycle a full meal of petrol, let us say one gallon, and run it until it stops, in general we find that it has lost weight roughly equivalent to the weight of one gallon of petrol at the end of the run. Of course, if allowed to run inexpertly, it may become tired before the petrol has given out. Insufficient lubrication results in overheating, or expansion of some essential fitting results in immobility. In the meantime the air around has also

suffered a change, sometimes more impressive to the pedestrian than to the cyclist. If the engine is running efficiently this change consists in the disappearance of a certain quantity of oxygen and the production of a certain quantity of water vapour and carbon dioxide. If the combustion is incomplete the motor-bicycle excretes soot. The rate at which a motor-bicycle breathes is regulated by the air control. In all these operations nothing is lost or gained in the net result. What the bicycle loses in weight, the air gains.

Living matter is no exception to this rule, as Lavoisier and Priestley, the discoverers of oxygen, first proved. To take the case of an ordinary man weighing about ten stone, kept in an airtight box and fed for a certain period (one day), a typical balance sheet is given by Haldane and Huxley.[1] Since oxygen disappears from the surrounding air, this must be placed, along with the food consumed and any gain of weight during the period, on the credit side. On the credit side we have :—

Food	1.1 kilos (60% water)
Drink	1.5 kilos
Oxygen	500 litres or 0.7 kilos

This makes a total of 3.30 kilos.

On the debit side we have to reckon with the fact that he excretes during the same period 1.3 kilos of water and 70 grams of solids in his urine. He loses 1.1 kilos of water by evaporation from the skin as sweat. He loses 425 litres of carbon dioxide or 0.82 kilos, making in all a net loss of 3.29 kilos. The difference of 10 grams represents exactly what he has gained in body-weight at the end of the experiment. The carbon dioxide that appears is, as first recognised by Lavoisier, equivalent to that which would be formed by the same amount of food (allowing for what is retained for growth), if burnt in a flash.

[1] *Animal Biology.*

If a human being—or a frog—is placed in a heat-proof box or calorimeter, the effect of any movements he may execute is to generate additional heat by friction with the surrounding atmosphere, and all the energy he releases will appear in the form of increased temperature in the calorimeter. When this experiment, which is now a commonplace of animal biology, is performed, two things are found ; firstly, that the amount of energy expended is definitely related to the amounts of weight lost, oxygen taken in and carbon dioxide given off ; secondly, the amount of energy generated over a definite period is equivalent to the heat which would be generated by combustion of the quantity of food consumed, if it were burnt in another calorimeter. To take again the case of a man of about ten stone, cited from Haldane and Huxley, a corresponding balance sheet for the energy expenditure over the same period would be drawn up somewhat as follows. The same amount of food as he takes, burnt outside the body, would yield 2,400 kilocalories. The total heat lost by the body during the period of experiment being 2,190 kilocalories, the difference represents a deduction, due to incomplete oxidation of food, which can be proved from analysis of the excreta to be equivalent to 150 kilocalories, leaving only 60 kilocalories to account for. This represents the increased potential energy of the body due to stored materials which appeared in the previous balance sheet as increased weight. Thus the machinery of living matter is subject to the two great mechanical principles of conservation of energy and matter. These apply to all man-made contrivances and all physical phenomena : that is why it is right and proper to speak of the *living machine*. We call a dynamo, a water mill, a steam engine and a motor-bicycle machines, because they transform energy in accordance with certain definite rules, which are known as the laws of Energetics. We call a frog a living machine because it transforms one form of energy

into other forms of energy in accordance with the same rules.

Chemistry of the body. To understand their food requirements we must bear in mind that frogs grow and reproduce their kind, and it is hence necessary to enquire into the chemical constituents of the animal body. The principal constituents of the animal body are, first, water—even man is at least 60 per cent. water; secondly, dissolved in the water, certain mineral salts—notably those of sodium, calcium, potassium and magnesium in the form of chlorides, bicarbonates and phosphates; finally, organic matter which can be classified under three principal headings, carbohydrates, fats and proteins. The *proteins* are the most important. They all contain carbon, hydrogen, oxygen and nitrogen: often sulphur and phosphorus. The molecule of a simple protein may be more than a thousand times heavier than the molecule of a compound like common salt.

The protein molecule is usually regarded as built up of large numbers of amino acids. An amino acid is an organic acid in which a hydrogen atom is replaced by an NH_2 group, *e.g.* amino-acetic acid is CH_2NH_2COOH. Fischer has synthesised a compound containing eighteen amino acid groupings. Such a compound is vastly simpler than the simplest protein, but we have moved a long way from the age when, in the very same year that received Wohler's announcement of the successful synthesis of urea, the great chemist Henry wrote (1827) concerning organic compounds:

> It is not probable that we shall ever attain the power of imitating nature in these operations. For in the functions of a living plant a directing principle appears to be concerned peculiar to animated bodies and superior to and differing from the cause which has been termed Chemical affinity.

The white of a fowl's egg is almost exclusively composed of the protein, egg albumen. Gelatin is another example of

a pure protein. Yet another is hæmoglobin, the red colouring matter of our blood. *Carbohydrates* contain carbon, hydrogen and oxygen only, the last two in the same proportion as in water. The simplest carbohydrates are the simple sugars, glucose and grape sugar. More complex sugars are formed by the union of two molecules of simple sugars. Such are cane sugar (the sugar we eat), malt sugar, and the sugar contained in milk. The union of several molecules of simple sugar gives rise to much more complicated compounds of the same class, known as starch, cellulose, dextrins, etc. Potato flour is largely composed of a starch. Rice paper is largely composed of a dextrin. Cellulose, which forms a large part of the dry substance of any plant, since all plant cells are enclosed in a wall of cellulose, and lignin, the substance of woody fibres, are also highly complex members of the carbohydrate class. The *fats* also contain the same three elements alone—at least the simpler ones do ; but in chemical structure they are quite different. A simple fat like lard or olive oil is an ester of the trihydric alcohol glycerine and one or more of the higher fatty acids (usually acids with at least sixteen carbon atoms).

With the exception of the sugars, all these essential constituents of the organic matter of the animal or plant body are either like the fats quite insoluble in water, or like the proteins and starches soluble but incapable of passing through animal or vegetable membranes (*e.g.* parchment) in the way in which common salt diffuses through them in solution : their molecules are too large. Before the food eaten by an animal can get through its tissues to its destination, it undergoes certain changes. This process is known as digestion.

Digestion. Frogs feed on worms, insects, and the like. These, like our own food and that of all animals, contain all three classes of essential organic compounds the body requires for growth and activity. It may be asked, where do

these come from in the first place? Those animals that do not feed on other animals are vegetarians; and plants possess a peculiarity of nutrition that animals do not. They can build up carbohydrates from the carbon dioxide and water of their environment and build up proteins as well. Since these are the things which supply chemical energy to the living machine, it may be asked, whence comes all the energy required to build up these stores of chemical energy? The answer is that plant tissues absorb light by means of the green colouring matter, chlorophyll, of the stem and leaves: only in the day-time can they build up starch. The ultimate source of the energy of life on this planet is therefore the radiant energy of the sun.

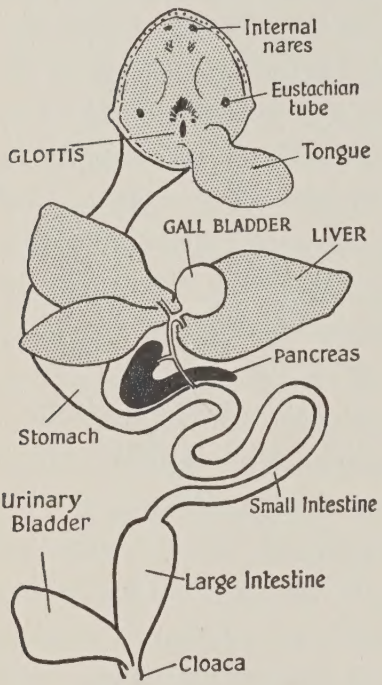

FIG. 34—ALIMENTARY CANAL AND ASSOCIATED STRUCTURES IN THE FROG

From the mouth the food swallowed by a frog passes into a winding tube which terminates in a second opening to the exterior, the *anus*, situated dorsally where the legs are joined to the body. This tube, known as the *alimentary canal* or digestive tract, has everywhere muscular walls, an inner layer of plain muscle fibres arranged circle-wise, and an outer coat with a lengthwise arrangement. The slow rhythmical movements of these muscles help to churn the food, and squeeze it along the alimentary canal to the anus. The inner wall is lined with an epithelium, which for a great part of its course consists partly of mucous secreting cells or is folded in pits which are of a glandular nature. The first part of the tube, which in our own case is

called the *oesophagus* or gullet, is hardly distinguishable in the frog from the stomach which follows. The stomach leads into a narrower tube, the intestine. The intestine of

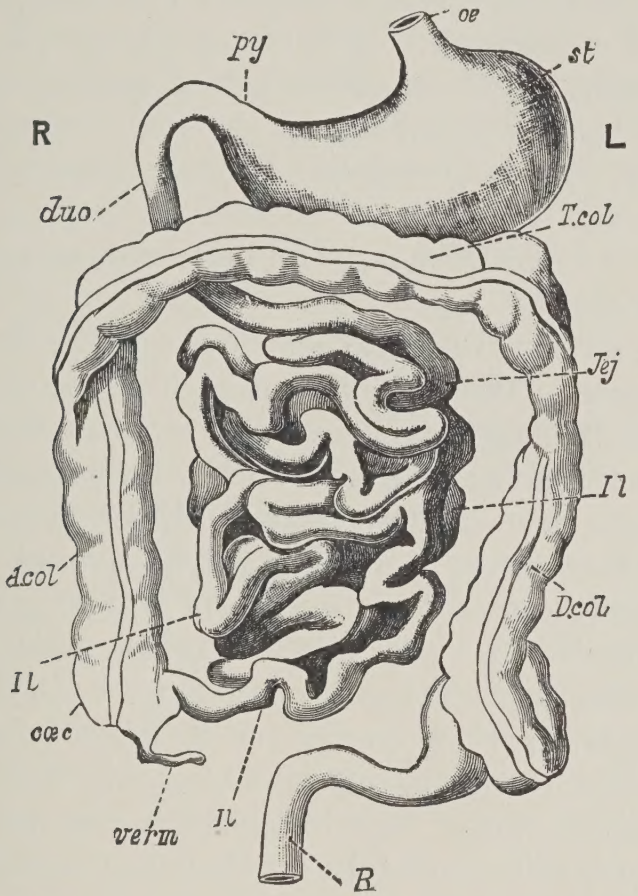

FIG. 35—THE ABDOMINAL PORTIONS OF THE HUMAN DIGESTIVE TUBE, VENTRAL VIEW

R, right ; L, left sides of the body ; *oe*, gullet (œsophagus) ; *st.*, stomach ; *py*, aperture of stomach into small intestine (pylorus) ; *duo*, duodenum, opening into the much-coiled remainder of the small intestine (*Jej* and *Il*). This opens into the large intestine, with its coecum (*coe*) and vermiform appendix (*verm*). It is divided into colon, ascending (*A. col*) and descending (*D. col*) and rectum (*R*).

the frog has two distinct portions, the coiled narrower *small intestine* and the short and wider *large intestine* or *rectum*. The rectum communicates with the exterior by way of a small pocket, the *cloaca*, that also receives the generative and urinary ducts.

The food in its passage along the alimentary canal of the frog encounters the various juices secreted by different parts of the walls of the digestive tract, and also the secretions of two larger glands, the liver and pancreas, which open by a common duct into the small intestine near its anterior end. These digestive juices contain substances known as *enzymes* which act on the complex organic constituents of the food, rendering them sufficiently simple to diffuse through the walls of the stomach or for the cells of the body to build them up into other substances as these may be required.

Enzyme action. Chemical reactions may be divided into two categories. One includes all such as are involved in ordinary methods of volumetric analysis, where the combination of reacting substances is practically instantaneous, as for instance, the neutralisation of hydrochloric acid with soda or the precipitation of barium sulphate from a soluble barium compound in the presence of free SO_4 ions. The other comprises a large number of organic reactions, such as the saponification of esters or the inversion of cane sugar, in which an appreciable period of time must elapse before the point of equilibrium is reached. The reactions with which the biologist is concerned belong pre-eminently to the latter class. Many reactions such as the combination of pure oxygen and hydrogen ordinarily proceed at an immeasurably slow rate, but can be induced to take place within ordinary time limits in the presence of certain substances (in this case, *e.g.* finely divided platinum), which do not appear to have undergone any change whatsoever at the conclusion of the experiment. For such bodies as are capable of influencing the velocity of a chemical reaction without entering into the composition of the end products, or, in general, shifting the point of equilibrium for a given set of conditions, the term *catalyst* is commonly employed. The facility and rapidity with which the organism

is enabled to disintegrate highly stable compounds, such as proteins, is due to the agency of a special type of catalyst known as *enzymes*, of which an example familiar to most people, owing to its commercial use, is the *rennin* of the gastric juice.

The term *enzyme* was introduced by Kuhne (1878) to obviate the confusion resulting from the use of the older term "ferment," a term originally used to include micro-organisms like the yeast fungus. This confusion was finally dissipated when Buchner (1903) extracted from crushed yeast cells an "unorganised" ferment capable of effecting the identical transformation hitherto associated with the activities of the living organism.

Apart from the fact that they are all derived from living organisms, it is difficult to fix on any single characteristic which will differentiate enzymes from all other types of catalysts. At present their chemical constitution is unknown. What may be described as the general catalytic properties of enzymes may be classified under three headings, the reversibility of their action, their efficacy in very small quantities, and the independence of the amount present to the final result. Of these the first is of special importance to the understanding of the chemical balance of the body, or, to use the term usually employed for the chemical processes of the organism as a whole, *metabolism*.

A straightforward illustration of what is implied by the term reversibility of reaction is provided by the preparation of ethyl acetate, which was the subject of the historic researches of Berthellot and Pean de Saint Gilles (1862) on mass action. If equal amounts of molar solutions of acetic acid and ethyl alcohol are brought into contact an equilibrium point is reached when the molecular concentration of the reacting compounds is reduced by two-thirds owing to the formation of ethyl acetate. Precisely the same

point of equilibrium is reached when a molar solution of ethyl acetate is subjected to acid hydrolysis, *i.e.* broken down by the catalytic action of a mineral acid. It is usual to think of both reactions as taking place continuously and simultaneously with different velocities except at the point of equilibrium concentration for the reacting substances. The catalyst, in this case an acid, acts by accelerating the reaction in either direction, and the equilibrium point for the same conditions of concentration, etc., is unchanged, so that the total energy of the system is unaltered. Theoretically any reaction may be regarded as reversible. In their efficacy to accelerate the velocity of reaction in either direction, enzymes conform to the behaviour of other catalysts. The first demonstration of this was due to Croft Hill (1898) who studied the hydrolysis of the disaccharide malt sugar under the influence of the enzyme *maltase*. Malt sugar is split by this enzyme into the simpler sugar *d-glucose* (a monosaccharide). Hill showed that when maltase is added to glucose, malt sugar is formed, and the equilibrium point is reached at the same relative concentration of the two sugars as in the reverse reaction for identical conditions. Needless to say, any reversible reaction may proceed to completion either way by the continuous removal of one of the end products by means, either mechanical (*e.g.* diffusion), or chemical (*e.g.* precipitation). Hill's discovery makes it possible to envisage how, for example, the balance of sugar in the body and glycogen in the liver and muscles is continuously maintained throughout life, or how, to take a second illustration, the tissues store up fat when the diet is plentiful, while in times of shortage fat disappears from them.

In true catalysis the final result of a reaction is not determined by the quantity of the catalyst present, though the extent to which it is accelerated is within certain limits affected. In a good many cases the enzyme can be reclaimed at the end of a reaction and made to react on a

fresh supply of material, as has been shown in the case of the starch-splitting enzyme, *amylase*. In other cases this is not so. Enzymes are highly unstable bodies, being readily destroyed, like many other colloidal systems, by heat. It appears in some cases that the final products of the reaction tend to disintegrate the enzyme, and it cannot be rediscovered at the conclusion of the reaction. Surprisingly small quantities of enzyme are efficacious. Rennet, the gastric juice extract employed domestically for the preparation of junkets and commercially on a large scale in the manufacture of cheese, is able to clot 400,000 times its own weight of the milk protein *caseinogen*. Even this figure gives an imperfect picture of the prodigious activity of the enzyme. The active constituent is very small in proportion to the bulk of the extract.

Digestive enzymes. The secretion of the stomach or *gastric juice* contains free hydrochloric acid; it also contains an enzyme *pepsin* which, either in the test tube or in the body, breaks down complex proteins, like albumen, into very simple proteins that are called peptones; it has no action on the starchy or fatty constituents of the food. The bile or secretion of the liver does not contain a digestive enzyme. It is largely excretory matter in the form of certain pigments; but its alkaline salts neutralise the acidity of the gastric juice, and greatly facilitate the emulsification of fats. The pancreas is the chief digestive gland. Its secretion contains three important enzymes. One called *amylase* breaks down starch or dextrin into malt sugar. A second called *trypsin* can break down proteins into the organic " amino " acids of which the protein molecule is built up. It thus carries protein digestion a stage further than that reached in the stomach. A third called *lipase* breaks up fat into fatty acid and glycerol. The intestinal juice secreted by the glandular walls of the small intestine also contains enzymes, one called *erepsin*, which acts on the final stages of

protein decomposition completing the work of the pancreatic juice, and a series of others which act on the complex sugars like malt sugar, converting them into simple sugars. Man possesses three pairs of *salivary* glands whose ducts open into the mouth. Our saliva contains an enzyme which in comparatively alkaline and neutral solution acts like the pancreatic amylase on starch. It cannot act in the acid medium of the stomach contents, and vigorous mastication, while probably an admirable means of preserving the teeth, has no justification on the grounds of facilitating starch digestion to any considerable extent. So far as is known, neither the digestive tract of man nor of the frog contain any enzyme that breaks down cellulose. This is a very strong argument against an exclusively vegetarian diet for either. In man, cellulose is broken down by bacteria in the large intestine, and is wasted. The cellulose wall of plant cells makes them much less accessible to the action of the digestive juices than animal tissues. The chief value of vegetable food lies in the fact that it can be eaten raw as a supply of certain constituents of a normal diet, the so-called vitamins, which are requisite in extremely minute quantities and have not as yet been identified chemically. The vitamin content of food is diminished by prolonged cooking.

Any undigested or indigestible matter eventually passes out of the body, along with the bile pigments that confer its characteristic colour, as fæces. In the small intestine the starches have all been absorbed as sugar by the fine blood vessels beneath its epithelium. The proteins have been broken down into the diffusible substances known as amino acids and travel to the tissues by the same route. The products of fat digestion on the other hand are taken up by the cells of the lining epithelium of the small intestine, and given up in turn to the underlying tissue spaces. The ensuing stage in the history of the foodstuffs, therefore, belongs to the subject matter of our next chapter on the cir-

culation of the blood. But first let us look at the other end of the story, the burning up of the final products of all the chemical activity that goes on in the body, and the removal of waste substances.

Respiration. Like ourselves, the frog takes in oxygen from its surroundings and gives up carbon dioxide. All parts of

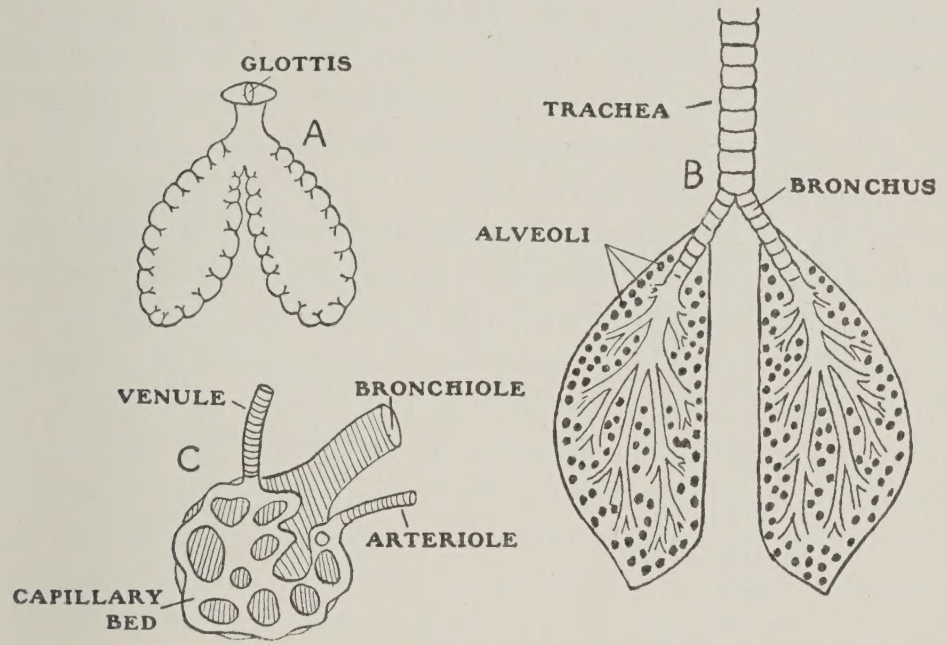

FIG. 36—RESPIRATORY ORGANS OF FROG AND MAN
A, lungs of frog. B, lungs of Man. C, single air sac or alveolus from human lung.

the body utilise oxygen in this way, but in ourselves oxygen enters the body by one route and one route only, namely the lungs. These are spongy sacs well supplied with blood vessels, the walls of their pores being very thin, and all its minute cavities, or alveoli, communicating with a tube—the *bronchus*—which joins its fellow of the other lung to form the organ known as the *trachea* or windpipe. Air is sucked through the nasal passage or mouth into the windpipe at the back of the throat by the suction of a broad sheet of muscle, the diaphragm, beneath the lungs and above the stomach. In the frog a good deal of absorption of oxygen and elimination of carbon dioxide takes place all over the surface

of the body through the moist skin. The lungs are less spongy than ours are and have relatively fewer compartments. The two lungs open together by a longitudinal slit, the glottis, at the back of the throat. The frog breathes by swallowing air. It has no diaphragm.

In the frog the main use of food is to supply chemical materials for the activities of the organs, *e.g.* glycogen or animal starch for the muscles, and materials for growing tissues. The frog is much less capable of surviving cold than we are. Man is a warm-blooded animal and maintains a temperature higher than that of his surroundings by the oxidation of foodstuffs. Man requires relatively more food than the frog for this reason. Though oxygen is essential for sustained muscular activity, the energy of muscular activity does not come from the oxidation of materials in the muscles. Muscles, as stated in the concluding section of Chapter II, will contract in the absence of oxygen. The energy of muscular movement comes from the breakdown of animal starch (glycogen) into lactic acid. If lactic acid accumulates, fatigue ensues. By burning up the lactic acid into carbon dioxide and water vapour, oxygen makes possible the removal of the fatigue products. In the efficient activity of an animal, non-volatile products of muscular work are burnt up as soon as they are formed. For this reason muscular exercise is quantitatively related to oxygen consumption in the normal course of events, and it has been customary in the past to regard the oxidation of the foodstuffs as the source of muscular energy. Strictly speaking, this conclusion is incorrect. It is none the less true that the disappearance of a fixed amount of oxygen is ordinarily associated with a given amount of muscular activity in the balance sheet of the living machine.

Excretion. Movement in the frog is the main form of bodily activity, and as muscle uses carbohydrate (glycogen) as its source of energy, it follows that in a full-grown

animal most of the nitrogenous material of the food is waste matter. The body can convert the products of protein digestion into carbohydrates by removal of the nitrogenous portion in the form of materials such as urea, $CO(NH_2)_2$. These are eliminated from the body in the urine. The urine is produced by two bodies known as the kidneys which communicate with the cloaca by tubes known

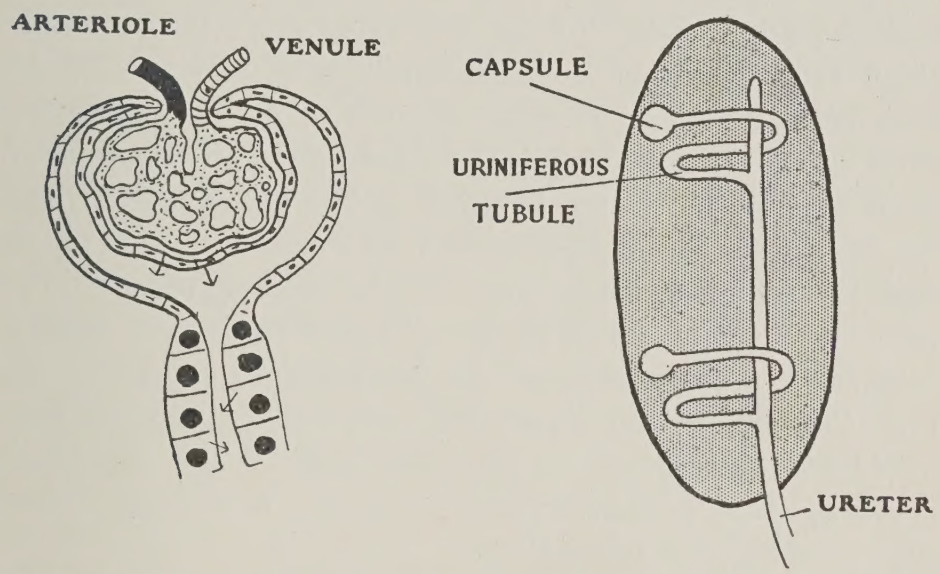

FIG. 37—ON THE RIGHT, VERY DIAGRAMMATIC REPRESENTATION OF THE KIDNEY OF THE FROG WITH TWO OF THE TUBULES SHOWN DISPROPORTIONATELY ENLARGED. ON THE LEFT, THE CAPSULAR END OF A SINGLE TUBULE, HIGHLY MAGNIFIED

as the *ureters*. Each kidney is a flattened ellipsoidal structure with a small cavity continuous with the canal of the ureter. Into this cavity open innumerable closely-packed tubules of glandular structure which make up the substance of the kidney. These tubules terminate in a flask-shaped swelling whose walls are invaginated to receive a tuft of small blood vessels, this portion being called the Malpighian body, or capsule, after Malpighi (1628–1694), one of the earliest microscopists. The structure of our own kidney is essentially like that of the frog in this respect, but in man

the ureters open into a capacious receptacle with muscular walls, the bladder. This communicates with the exterior by a duct called the *urethra*, separately in the female and along with the male generative ducts in the male.

History of digestion and respiration. We have said nothing so far about the history of metabolism. The chemistry of the animal body could not be studied at all until comparatively recent times, and in point of fact the applicability of the two great scientific generalisations known as the indestructibility of matter and the conservation of energy were applied to animals almost as soon as they were recognised to hold good in the world of dead matter. Towards the end of the eighteenth century the ingenious Abbot Spallanzani made observations on the digestion of meat in the stomach by making dogs swallow pieces of meat attached to string, and withdrawing them at intervals. He also showed that the gastric juice would perform the same action outside the body. Under the influence of Liebig and others in the first half of the nineteenth century, the foundations of modern knowledge about digestion had been laid down.

It was the experiments of Robert Boyle with his air pump that showed the necessity of air to animal life, and John Mayow in the first half of the eighteenth century clearly recognised that only a part of the air was so essential. The history of the study of respiration is closely bound up with the discovery of oxygen, nitrogen, hydrogen and carbonic acid gas. An excellent account will be found in Foster's *History of Physiology*. Black, the discoverer of carbon dioxide, and Priestley, whose experiments on oxygen antedated the real discovery of the latter by Lavoisier, were both intensely interested in the problem of respiration. Two years after his epoch-making work on the calcination of metals, Lavoisier published (1777) the first of a series of memoirs on animal respiration, recognising at the outset

the essential fact that the carbon dioxide exhaled from the lungs was the product of an oxidation process, in which the source of oxygen was the atmosphere. In 1780, in collaboration with the great mathematician Laplace, Lavoisier published a memoir on animal heat, showing by direct physical measurement with the balance and the thermometer that the warmth of our bodies is a process of combustion of a kind essentially like that of the candle flame. After the discovery of hydrogen by Cavendish, Lavoisier further discovered that water vapour as well as carbon dioxide arises from the oxidation processes of the body. In 1803 Spallanzani published a memoir recording large numbers of experiments on a variety of animals (vertebrate and invertebrate) showing that the phenomena of respiration are universal properties of the animal economy, and that the seat of the respiratory processes is the tissues themselves.

Chapter V

THE TRANSPORT OF MATERIALS IN THE ANIMAL BODY

OUR last task was to enquire into the sources of energy of the animal body. We saw how chemical materials containing a rich supply of stored energy are taken into the body, and how oxygen supplies the body with heat and burns up the end-products of muscular activity. We have still to enquire how the digested food materials are carried to the tissues from the walls of the gut, how oxygen is transported from the lungs to the tissues, and how carbon dioxide is transported from the tissues to the lungs. So we come to a consideration of the circulation of the blood.

If we examine the translucent skin between the toes of the frog we find that it is threaded with a network of fine tubes, through which a reddish fluid, the blood, is visibly moving. Through this network we are able to see that the flow of the blood is in a definite direction, and we can easily observe that the finer vessels are formed by the repeated division of larger vessels and that in their turn these unite together to form other vessels which are also larger. The smallest vessels of the network are called *capillaries*, and a network of similar vessels is found in all parts of the body. Capillaries unite together to form larger vessels with muscular walls called *veins*, which have little valves in their course, rather like watch pockets (Fig. 38). If we trace the smaller veins of any organ forward in the direction in which the blood is moving

we come, sooner or later, to the large muscular pumping organ known as the heart. From the heart spring vessels thicker than the veins and without valves, except at the point where they leave the heart itself. These are called *arteries*. These arteries branch repeatedly, and eventually their terminal branches are continuous with the capillary network of the various tissues of the body. Thus the blood flows in a closed circuit, from the heart *via* the arteries to the capillary network of the tissues, and from the capillary network of the tissues by way of the veins back to the heart itself.

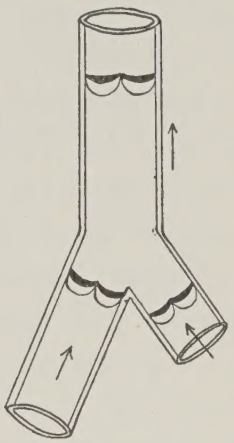

FIG. 38—DIAGRAM OF VEIN SHOWING VALVES

The arrows represent normal direction of the flow of blood.

The fact that the blood of man and animals generally, if they possess a circulatory system, flows in a closed circuit, was not fully grasped before the work of Harvey in the seventeenth century (1628), though some earlier anatomists, including Servetus who was burned at the stake at the instigation of Calvin, had come very near to a clear realisation of the fact. Until the invention of the microscope, it was impossible to see the finer vessels. The circulation was first observed directly in the manner indicated above by the pioneer microscopists Malpighi (1661) and Leeuwenhoek (1668).

The Blood. Blood is not a homogeneous fluid, but a suspension of densely packed cells. Some of these are ovoid discs charged with a colouring material which in thin layers is yellowish, but seen in greater concentration appears red. This colouring matter which gives to blood its characteristic hue is known as *hæmoglobin*. A solution of hæmoglobin is normally of a bright scarlet hue, like that of the blood in our arteries. When shaken in a

vacuum or in pure nitrogen or hydrogen, it changes colour, as was first shown by Priestley (1774). It assumes the purple hue of the blood flowing in the veins. Priestley also succeeded in showing that oxygen, or, as he called it, dephlogisticated air, was the constituent of the atmosphere with which purple, or reduced hæmoglobin combines. The presence of hæmoglobin is thus a fact of immense importance. Owing to its power to combine loosely with oxygen, the amount of oxygen that blood can take up is considerably higher than the amount which dissolves in a corresponding quantity of water. Thus 100 c.c. of our own blood will take up 18.5 c.c. of oxygen in air at atmospheric pressure, whereas 100 c.c. of water would absorb only 0.7 c.c.

The movement of the blood in the vessels ensures a constant supply of food materials and oxygen to the tissues, and a constant draining away of waste products which diffuse through the thin walls of the capillaries. It is the oxygen-carrying property of the blood which is specially important. All tissues store food materials, just as the muscle stores glycogen or animal starch. But the storage capacity of the cells of the body for oxygen is very small, and oxygen is constantly being used. Insects which have a peculiar system of minute tubes (tracheæ) bringing air directly into contact with the tissues can get on perfectly well without a well-developed circulatory system, though many insects surpass all animals except birds in their incessant muscular activity. Hæmoglobin occurs in the blood of all the great groups known as Vertebrates (fishes, frogs, lizards, birds, man, etc.) and in most of the worms. The blood of snails, lobsters, squids and a few other animals contains another respiratory pigment, known as *hæmocyanin*, which is blue in the presence of oxygen, and becomes colourless when shaken in a vacuum. Hæmocyanin, like hæmoglobin, is a protein combined with a metal, in the

former case copper and in the latter iron. Hence the importance of traces of iron in our own food.

The Circulatory System of the Frog. A convenient starting place to take in considering the circulation is

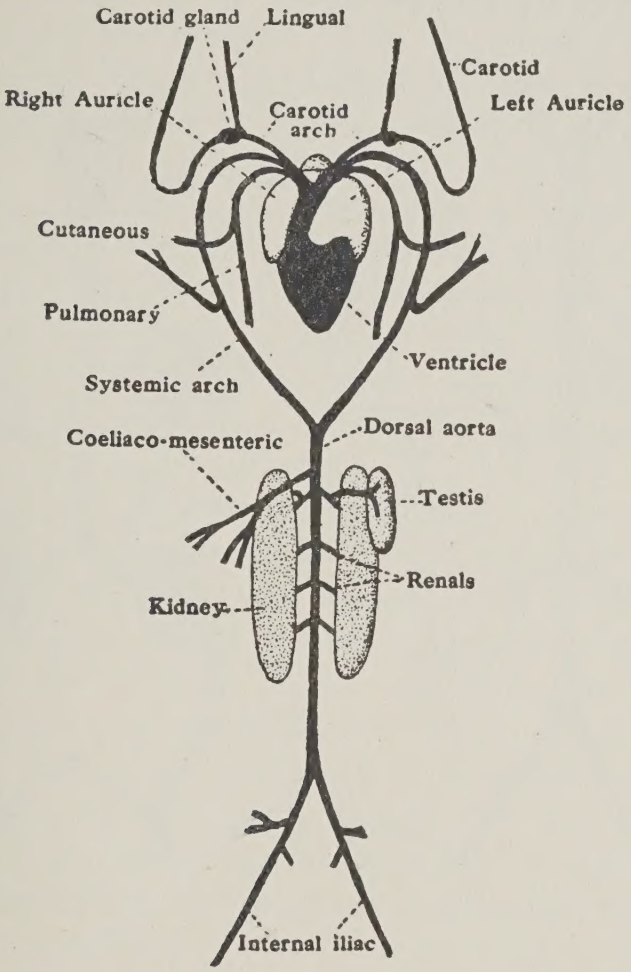

FIG. 39—PRINCIPAL ARTERIES OF THE FROG

the capillary network of the digestive tract. The small veins of the intestine unite into larger ones which eventually merge into the vessel known as the *hepatic portal* vein. This vein does not unite with other veins directly, but branches in the substance of the liver into smaller veins which are continuous with the capillary network

of that organ. The liver is a great storehouse of carbohydrate in the animal body. It stores carbohydrate in the form of the animal starch known as glycogen. The blood coming from the capillaries of the intestine after a meal is ordinarily rich in sugar. In the liver the excess of

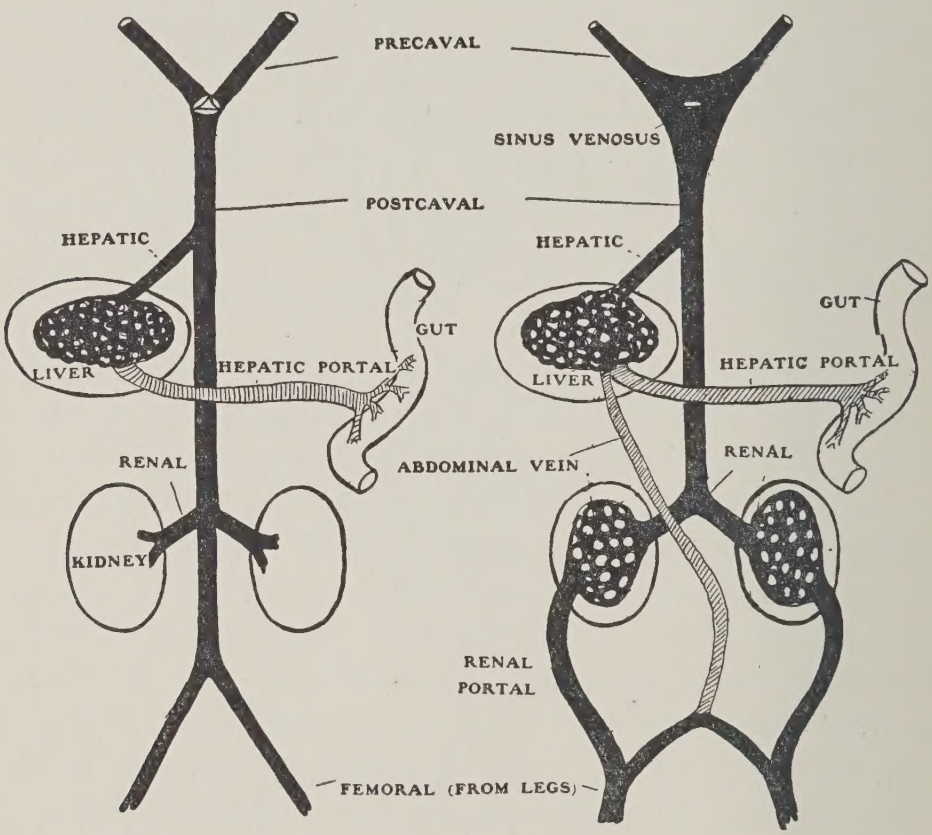

FIG. 40—MAIN VEINS OF FROG (RIGHT) AND MAN (LEFT)

sugar is built up into glycogen. The glycogen of the liver is transformed into sugar, as the supply of glycogen in the muscles is used up. The work of Claude Bernard in 1857 first showed that the blood in the hepatic portal vein after a meal is richer in sugar than the rest of the circulation, and that the store of glycogen in the liver goes down during starvation and increases immediately after the assimilation of food.

The blood in the capillary network of the liver is collected by small veins which join to form the two *hepatic veins*. These flow into a large vein, known as the *postcaval* or inferior vena cava, that picks up blood from the kidneys and discharges it into the thin-walled chamber of the heart known as the *sinus venosus*. Into the sinus venosus flow two large veins from the head and fore limbs, known as the *precavals* (right and left). The principal tributaries of each precaval are the *jugular* veins, bringing back blood from the head, the *subclavian* veins bringing back blood from the capillary network of the arms, and the *musculo-cutaneous* which bring back most of the blood from the skin of the trunk. Apart from the lungs we have still to account for the blood which returns to the heart from the lower limbs, and this has been left to the last, because in this respect the venous circulation of the frog is somewhat different from that of the human being. In the frog the veins of the leg, the principal one of which is called the *femoral* vein, breaks up in the capillaries of the kidney, just as the hepatic portal vein breaks up in the capillaries of the liver, whereas the veins of the leg in the human being merge into the postcaval directly. There is, as far as we know, no special advantage in this feature (the *renal portal* system) of the frog. Not all the blood from the legs of the frog passes back to the heart through the renal portal system. Two vessels from the femoral veins meet in the mid-ventral line to form a conspicuous vein running up under the muscular wall of the trunk. This vessel, the *abdominal* or *epigastric* vein, discharges like the hepatic portal into the capillary bed of the liver. It is not present in the adult human being, but is represented in the human embryo. The most important fact about the venous circulation of both the frog and man, and we might add of fish or fowl, is the hepatic portal system, that is to say, the fact that all the blood returning from the alimentary tract

passes through the capillary network of the liver en route for the heart. The glycogen-storing activity of the liver is its most important rôle in the economy of the body. In human beings the liver stores a good deal of fat. The frog possesses special masses of fatty tissues, the fat-bodies attached to the kidneys. These diminish greatly in size during hibernation (winter sleep), when no food is available.

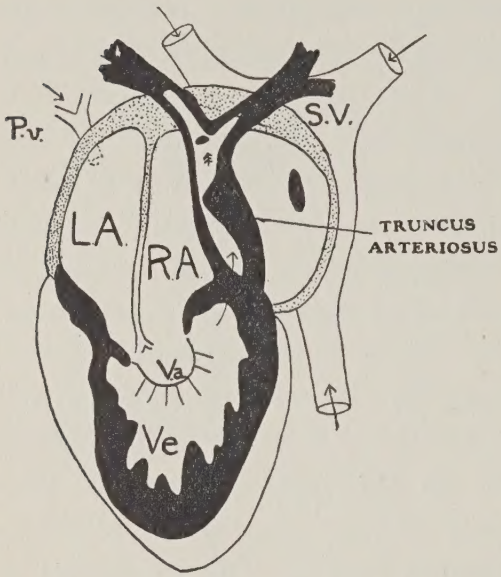

FIG. 41—THE HEART OF THE FROG

We have now referred to the larger veins which bring back blood from the capillaries of all parts of the body except the lungs. We have next to describe the structure of the frog's heart. The heart of the frog consists of three portions, the *sinus venosus*, a thin-walled chamber into which the pre- and postcaval veins pour blood; a portion, the *atrium*, with slightly thicker walls, divided completely into two chambers, the right and left *auricles;* and a very thick-walled chamber, the *ventricle*, which pumps blood out into the arteries. The sinus venosus opens into the right auricle. Into the left auricle open two small veins, the *pulmonary* veins from the right and left lungs. Both auricles discharge into the ventricle. Between the auricles and the ventricle is a flap of fibrous tissue connected by fine cords of tendon to the inner wall of the latter. This is called the *auriculo-ventricular valve*. The whole of the heart is composed of muscular tissue, and it will continue to beat when it is removed from the body, devoid of all connection with the nervous system. The chambers of the heart contract and relax in orderly

succession, the sinus venosus first, the auricles next, and the ventricle last. The contraction of the sinus venosus forces blood into the right auricle. When the auricles contract blood is forced into the ventricle. As the latter fills up, the auriculo-ventricular valve floats upward, so that, when the ventricle contracts in its turn no blood can pass backwards into the auricles.

From the ventricle a single arterial trunk, the *truncus arteriosus*, emerges, and on either side it divides into three large arteries (Fig. 39). The most anterior of these is the *carotid* whose ultimate branches end in the capillaries of the head region, the most posterior is the *pulmo-cutaneous* supplying the lung, and sending a small artery to the skin of the trunk, and the middle one, known as the *systemic*, supplies a larger area, and requires more detailed description. Each systemic gives rise to a *subclavian* or *brachial* artery, which runs outward to the forelimbs, where its ultimate branches terminate in the capillary network of that region. The two systemics meet in the middle line of the body, dorsal to the postcaval vein, to form a single median artery, the *aorta* or *dorsal aorta*. From the dorsal aorta springs one large median artery, the *cœliaco-mesenteric*, whose terminal branches end in the capillary network of the gut and liver, etc., paired *renal* arteries, whose final ramifications end in the capillary network of the kidneys; and a pair of *iliac* arteries which supply the hind limbs.

The arteries have thicker walls than the veins, and except at the point where the carotid, systemic and pulmonary arteries leave the truncus arteriosus, and at the origin of the latter from the ventricle itself, they have no valves like those which are found in the veins. The blood in the arteries is at a much higher pressure than the blood in the veins. Blood spurts from a cut artery and trickles from a vein. The reason for this is that the fine tubes of the capillary network offer a considerable frictional resistance to the flow of the

blood, as is easily appreciated when we remember how hard it is to blow air or water through a very fine jet. In consequence the energy of the blood-flow in the veins (Fig. 42) is much less than in the arteries, and the presence of valves in their course ensures that the blood cannot flow back, when the arterial pressure falls while the ventricle is relaxing in the act of filling.

Regulation of blood-flow. The amount of blood flowing through an organ varies. To some extent it is adjusted to the oxygen requirements of the moment. Other things being

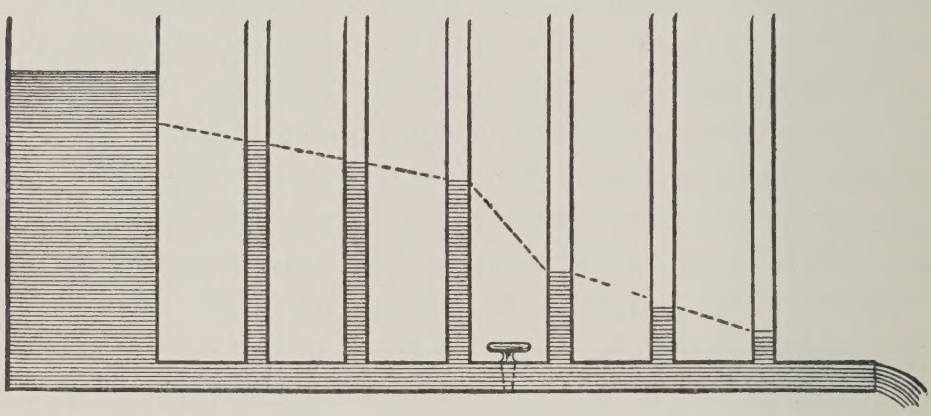

FIG. 42—PHYSICAL MODEL

To illustrate resistance of the capillaries to arterial pressure. An additional resistance is introduced by the small bore of the tap in the course of the horizontal outlet.

equal, the rate at which a tissue can take up oxygen depends upon the amount of blood which flows through it in unit time. Now the flow of a liquid through a tube of uniform bore depends upon the force propelling it, the length traversed and the sectional area of the tube. Only the first and last of these need be considered in connection with the circulation since the length of tube traversed is approximately constant in the blood vessels. As the activity of the heart is an intermittent quantity, the average force of the heart-beat depends partly on the frequency of the beat, or pulse rate, and partly on the amplitude or strength of the individual beats. Heart muscle reacts to

stretching by increased frequency and amplitude of beat, so that any increase in the resistance of the finer blood vessels calls forth more powerful action on the part of the pumping organ. Furthermore the heart is regulated by two sets of nerves, branches of the sympathetic system and the vagus respectively. The former discharge impulses tending to augment and the latter to inhibit the heart beat. The increased pulse rate following excitement or excessive exercise is due to the action of the former. The variations of heart rhythm that are thus possible affect only the circulation as a whole. Changes in the blood supply of single organs are possible on account of the fact that both the arteries and the veins, like the intestine, have walls with a double coat of plain muscle, one coat with the fibres arranged circlewise and one with the fibres arranged lengthwise. The extent of contraction of these muscle fibres is under nervous control, and any change in the extent of contraction of the muscular walls of the blood vessels means that the diameter of their bore is increased or diminished. The capillaries have no muscle fibres in their walls which are formed of a single layer of cells. The latter possess a measure of contractility. Blushing results from dilation of the smaller arteries and capillaries of the skin of the face. Loss of heat from the surface of the body, when exposed to cold, is compensated by constriction of the blood vessels of the skin, hence the whitening of the surface after bathing in very cold water. Sometimes the capillaries remain dilated while the smaller arteries are almost completely closed up. When this occurs, stagnant pools of blood occur in the capillary network and as their oxygen is used up the blood itself becomes completely reduced. This is what happens when the tips of the fingers become blue on a cold day. The blood of the frog is never warmer than the atmosphere, and the animal cannot withstand either great cold or high temperatures at which we can easily live.

Our blood is kept at a constant temperature (about 37° C.) in ordinary circumstances, and when we are exposed to a warmer temperature, secretion of sweat takes place. The evaporation of sweat from the surface of the body absorbs heat, thus keeping the surface cool.

The Lymph. Except in the spleen, a structure concerned with the removal of effete red corpuscles, the blood does not come into direct contact with the tissue cells. It is separated therefrom by the thin wall of the capillary bed, which is one cell layer in thickness. The spaces between the tissue cells are filled with a clear fluid, *lymph*, containing white corpuscles. Chemical exchange takes place between the cells and the lymph on the one hand and the lymph and the blood on the other, by physical diffusion. In the frog there are large lymph spaces between the skin and the muscles, and in addition to the abdominal cavity or peritoneum and the cavity around the heart or pericardium, a large lymph space in which the kidneys lie is separated by connective tissues from the abdominal cavity proper. In man the lymph spaces in the absorptive wall of the intestine, known as *lacteals*, communicate with a well-defined channel, the *thoracic duct*, which opens into the jugular vein. The lacteals are so called because after a meal of fatty constituents they are found to be gorged with droplets of fat, and it seems that the bulk of the fatty portion of the food is absorbed into the circulation by this indirect route. In the course of the lymph spaces there occur masses of dividing cells which are manufacturing new white blood corpuscles. These are spoken of as *lymph glands* and are usually enlarged in inflammatory conditions. The tonsils are large lymph glands. The red blood corpuscles are manufactured in the bone marrow. In the lymph space on either side of the urostyle of the frog there occur small strands of striped muscle which contract rhythmically, and are called the *lymph hearts*. Their pulsation can be easily

detected through the skin in the intact animal, but their precise significance is not clearly understood.

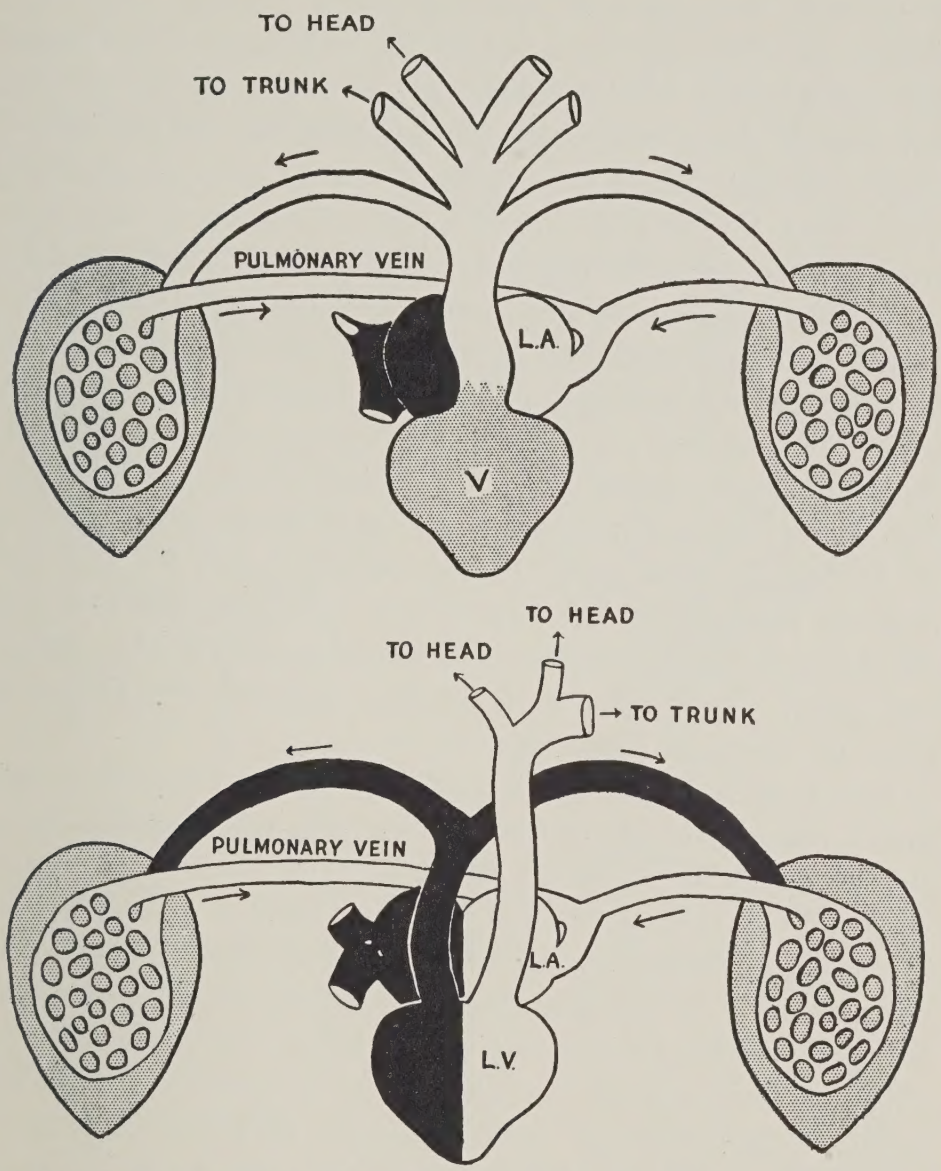

FIG. 43—THE RELATION OF THE HEART TO THE LUNGS AND TISSUES
Above—in the frog. Below—in Man.

The Human Circulation. The circulation of the frog differs in several respects from that of the human being, and of all warm-blooded forms. It is much less efficient

as a means of discharging the principal office of the circulatory system, the transport of the respiratory gases. Both the deoxygenated purple blood coming from the tissues of the body as a whole *via* the right auricle and the oxygenated blood returning from the lungs *via* the left auricle have plenty of opportunity for mixing in the single ventricle which pumps blood out into the arterial system. But the human heart is four-chambered. Its ventricle is completely divided into two. From the right ventricle the pulmonary arteries supplying the lungs emerge. From the left ventricle there springs an artery which divides to form paired carotids, paired subclavians and the aorta itself. Blood coming from the capillaries of the trunk, limbs or head passes into the right auricle, thence into the right ventricle, thence by the pulmonary arteries to the capillary network of the lungs, thence by the pulmonary veins to the left auricle and out of the left ventricle by the carotid, subclavian and aortic trunks to the rest of the body. Thus all the blood that supplies the tissues is fully oxygenated (Fig. 43).

The frog is in reality a half-way house between a fish and a human being. In its tadpole life the frog has a circulatory system essentially like that of a fish. At a certain stage of our embryonic life, we, too, have a circulation of this type, succeeded by one that is very much like that of the adult frog. The fish is an animal that breathes oxygen dissolved in water by passing a current of the latter through slits in the sides of the throat. These are provided with filaments richly supplied with capillaries and known as gills. The fish heart is single throughout ; the atrium is not divided into two separate auricles. All the blood from the body entering the heart is deoxygenated, and passes from the ventricle into a median artery which pumps blood by a paired series of arteries to the capillaries of the gills. Thence they are collected by arteries which join to form the aorta (Fig. 45).

Many fishes have a structure, known as the swim-bladder, by which they adjust their specific gravity. In a few fishes, such as the lung-fishes, it opens into the throat and is used as a lung. The lung of these fishes is supplied by an artery from the last of the gill arches. This represents precisely the arrangement in the frog just before it develops

FIG. 44—DIAGRAM OF GILL ARCHES AND HEART OF A TYPICAL FISH (right), AND TADPOLE OR LUNG FISH (left)
The gill clefts are seen on one side and the gill capillaries schematically on the other.

its limbs and sheds its tail, and it corresponds with the stage in our own development, when we possess gill-clefts like a fish. When the frog undergoes metamorphosis the median artery which gives rise to the paired gill arteries persists as the truncus arteriosus. The last gill arch loses its connection with the aorta, persisting as the pulmocutaneous, and the one immediately in front persists as the systemic by absorption of its capillary network. Such a stage exists in our own development. At an early stage the human embryo has *pharyngeal clefts* like those of a fish or tadpole, but they do not actually

carry gill filaments. Later the truncus arteriosus becomes progressively shorter, so that the pulmonary, systemic and carotid trunks come off directly from the ventricle, within

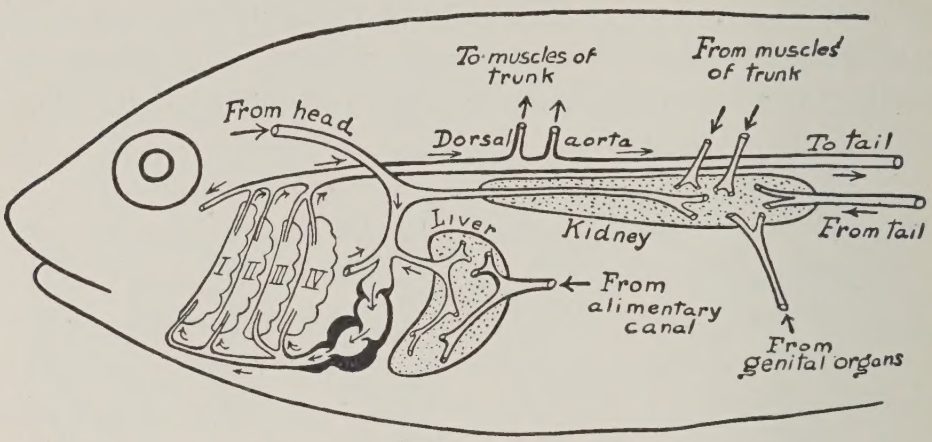

FIG. 45—CIRCULATION OF A FISH

which a septum is formed. In reptiles (lizard and tortoise, etc.) there is no truncus arteriosus, and there is an incomplete septum in the ventricle, but both systemics persist. In birds

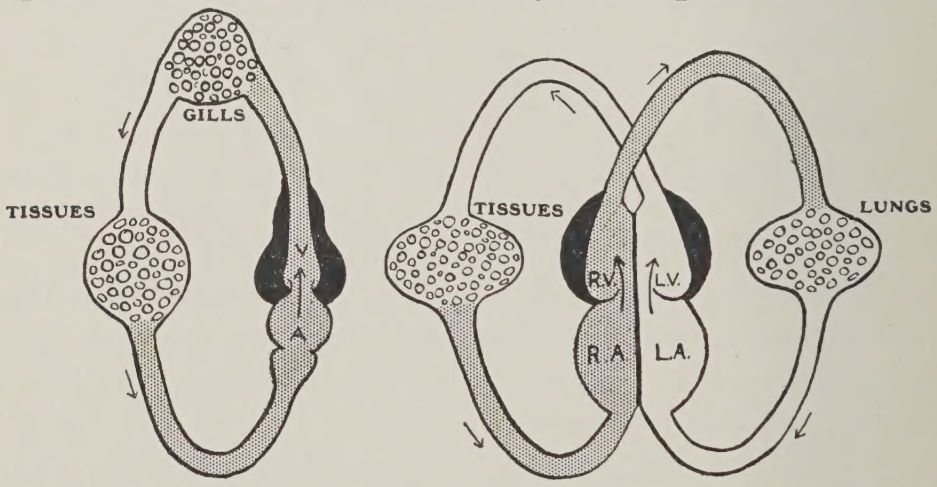

FIG. 46—DIAGRAMMATIC REPRESENTATION OF THE OXYGENATION OF THE BLOOD IN FISH (left) AND MAN (right)

the ventricle is completely divided, as is our own heart, but the single aorta is on the right side of the heart and not on the left, as in man (Fig. 48).

The ductless glands. The blood of the frog and of man plays

one part in the activities of the body which we have not referred to at all. We have already seen what an important part the nervous system plays in co-ordinating the responses of an animal with the events occurring around it. There is another kind of co-ordination that is sometimes called chemical co-ordination. It is a matter of common knowledge that certain chemical substances, generally called drugs, obtained from the tissues of plants, have very characteristic effects on certain organs of the body. For

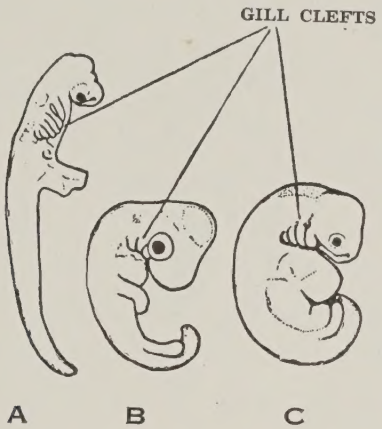

FIG. 47—EMBRYOS OF (A) SHARK, (B) BIRD, (C) MAN AT THE STAGE WHEN THE GILL CLEFTS ARE FORMED

The gill clefts never become completely perforated in birds and mammals, but skeletal and circulatory arrangements of the fish type are temporarily associated with them.

instance the drug known as caffeine, present in small quantities in coffee, promotes secretion of urine. Certain organs of the body produce drug-like substances called *hormones*, which, when carried by the blood stream to other parts, are capable of calling forth very specific responses, and in this way the circulatory system plays a part in co-ordinating response and stimulus.

The first discovery of chemical co-ordination was made by Bayliss and Starling in 1902. The pancreas does not secrete its digestive juice continuously, but only as a definite response to the entry of the acid food from the stomach into the intestine. Now the secretion of pancreatic juice

follows after the introduction of food or acid alone, even when all the nerve connections between it and the intestine are severed. Bayliss and Starling found that if the lining of the intestine is ground up with a little weak acid the concoction, when injected into the circulation, produces immediate flow of pancreatic juice. They, therefore, concluded that acid liberates a substance, which they called

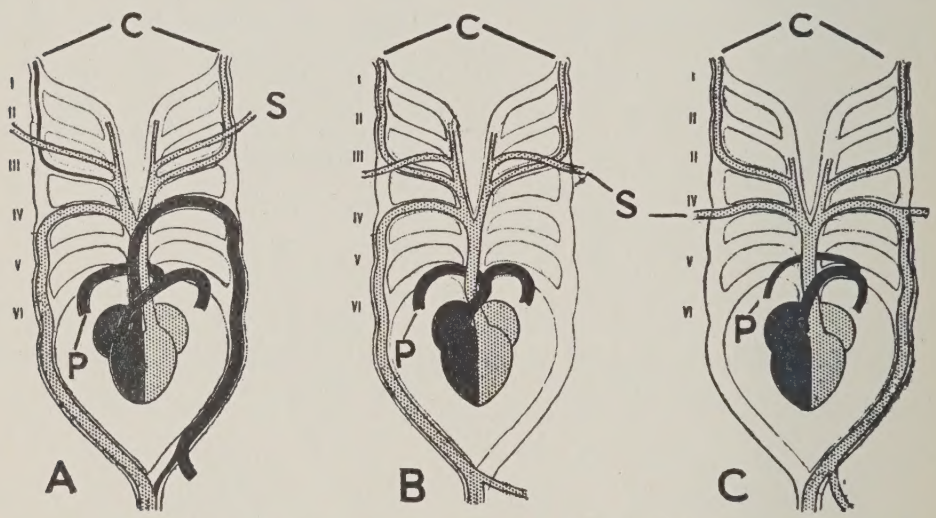

FIG. 48—ARTERIAL ARCHES OF REPTILE (A), BIRD (B), AND MAMMAL (C)

The Roman numerals refer to the embryonic arches. C, carotid artery; S, subclavian artery; P, pulmonary artery. Vessels carrying deoxygenated blood are shown black.

secretin, from the intestinal mucous membrane into the blood stream, whence it is conveyed to the pancreas and there evokes the characteristic response. This substance has now been prepared in chemically pure form. Bayliss and Starling's first experiments were performed with dogs. But they later showed that secretin is present in the intestinal wall of the toad.

An example of chemical co-ordination that has been worked out in frogs and toads is the control of colour response in these animals. We know that they change colour according to temperature, illumination, humidity, etc., and that they change uniformly over the whole body.

We know also that nerves convey to the central nervous system the impulses set up by appropriate stimuli in their surroundings. It was at one time thought that the nervous system transmitted these impulses directly to the melanophores or black pigment cells. This is not the case. In fact it is doubtful whether the melanophores of the frog have any nerve supply. Beneath the brain within the skull there lies in the frog and in man himself a little gland which has no duct conveying its secretion to the exterior.

FIG. 49—MICROSCOPIC SECTION OF THE THYROID GLAND

Showing follicular cysts lined by cubical epithelium and filled with a jellyish material.

Extracts made by grinding up this organ, the *pituitary gland*, in salt solution have some very remarkable properties. In particular, when injected into a pale frog, they bring about within half an hour a complete darkening of the skin resulting from expansion of the melanophores (Frontispiece). There is enough of the active constituent in one gland to bring about darkening in a hundred individuals. When the pituitary gland is removed, the frog recovers and survives, but in whatever circumstances it is kept, it will always remain completely pale. Darkening of the skin in a frog from which the pituitary gland has been extirpated can only occur, if a small quantity of the extract of the pituitary gland (about equivalent to one-millionth of a gram of the gland substance) is introduced into the circulation by injection. It thus seems that the nervous system controls the behaviour of the pigment cells by increasing or diminishing the rate at which the pituitary body pours its secretion into the blood.

Over the surface of each kidney there is an orange-coloured

mass of tissue, the *adrenal body*. It contains a drug-like substance that acts on plain muscle, in some cases relaxing and in others inducing contraction or increased rapidity of an inherent rhythm (*e.g.* it accelerates the heart of the frog). This substance, adrenaline, can now be manufactured in pure form in the laboratory. It is liberated into the circulation in small quantities, but we are not as yet certain under what conditions. The adrenal and pituitary bodies are sometimes spoken of as *ductless glands*. A third ductless gland, the thyroid, is dealt with in the next chapter.

Chapter VI

THE DEVELOPMENT OF A NEW ORGANISM

IN the first chapter three characteristic features of living matter exemplified by the common frog or a human being were distinguished. The manifold *reactivity* and *receptivity* to external influences have been studied in relation to their structural basis. The structural aspect of *reproduction* has only been referred to in a preliminary way.

We have now studied the part played by the various structures of the body of such an animal as the frog in its everyday behaviour. We must next consider for a short space the process of building up a living creature. The development of the egg of a frog has a very great advantage over that of other forms as an aid to understanding the way in which the complex architecture of the body is built up, for some of the most important features of the process can be followed with no more elaborate apparatus than a simple hand lens. A few hours after fertilisation, divisions of the egg into separate compartments or *cells* follow in rapid succession (Fig. 5). The egg at the time of fertilisation shows a concentration of black pigment towards the uppermost pole. The first division is parallel to the vertical axis, and the second is also in a vertical plane. The third division is in the horizontal plane, and separates off a tier of cells which contain black pigment from a tier of somewhat larger colourless cells. Successive divisions take place in all planes. A hollow sphere of cells of which the lower

half are relatively larger and contain no black pigment is thus formed.

Development of the frog. Up to this stage the only hint of any differentiation of the immature being, or

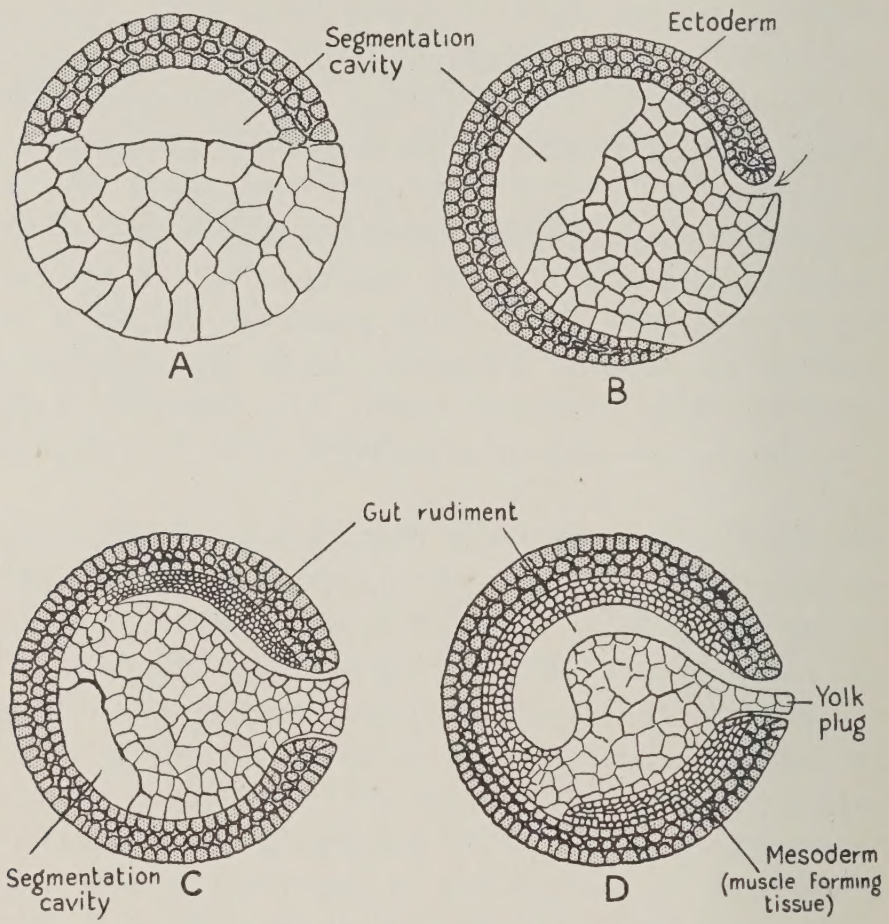

FIG. 50—FOUR EMBRYOS OF FROG

Showing stages in excavitation of the primitive gut.

embryo, as it is now called, into separate tissues or organs is the definite demarcation between the upper zone of smaller black cells and the lower zone (Fig. 50 A) composed of a somewhat irregular mass of cells rich in storage material or yolk. Now begins the stage of differentiation. Soon almost the entire surface of the embryo is covered with a layer of small pigmented cells, the larger

unpigmented cells being evident only at one end, the *yolk plug*. This is the future posterior end of the young organism.

FIG. 51—(1) POSTERIOR, (2) ANTERIOR, AND (3) DORSAL ASPECT OF THE FROG EMBRYO AT THE STAGE WHEN THE NEURAL GROOVE IS CLOSING UP

From now onwards we see the beginning of the differentiation of two systems of organs characteristic of the adult animal—the alimentary canal and the central nervous system. The black outer covering of cells forms a distinct lip over the yolk plug on one side. A small chink beneath this lip

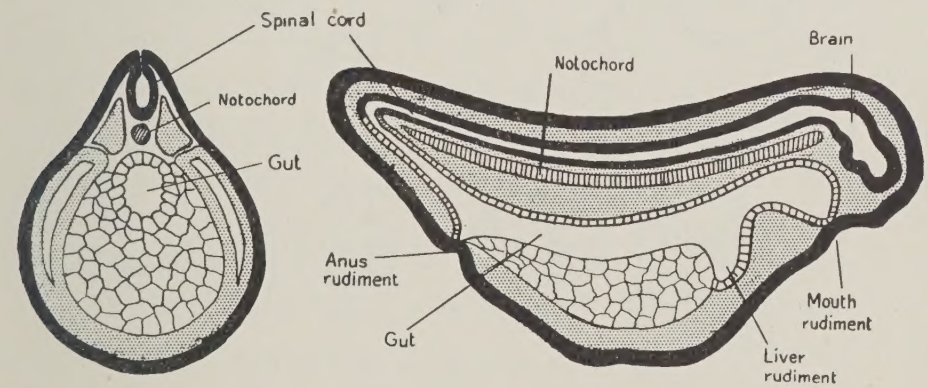

FIG. 52—TRANSVERSE AND LONGITUDINAL VIEWS OF FROG EMBRYO SHORTLY BEFORE HATCHING

grows inwards enlarging as it grows. This is the beginning of the alimentary cavity (Fig. 50 B–D) of the tadpole ; it is the embryonic gut. Meanwhile a groove appears on the surface of the embryo from the region (Fig. 51) just above the lip referred to. The groove is wider in front, and as it deepens,

its edges grow up, and coalesce, so that a tube is formed beneath a thin covering of cells. This tube, broadest at the future head end, is the rudiment of the spinal cord

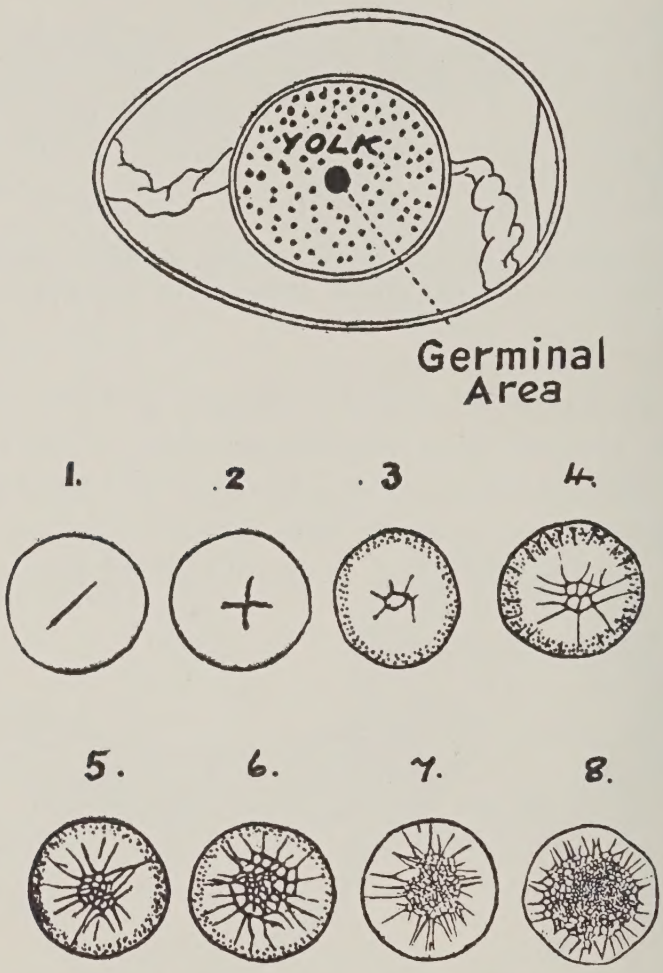

FIG. 53—THE EGG OF THE FOWL

Above—Whole egg showing position of the germinal area in which the nucleus is located at the time of fertilisation. Below—Stages in the cleavage of the germinal area as the egg passes down the oviduct, and is invested with the albumen and shell.

and brain. While this has been going on, cavitation of the mass of internal unpigmented cells has progressed inwards from the yolk plug. The original cavity of the sphere has become obliterated, and the new cavity excavated inwards from the yolk plug is destined ultimately to become

the cavity of the alimentary canal. As this cavitation proceeds, a belt of cells is separated off from the mass of colourless cells which form the innermost part of the embryo. This belt of tissue (*mesoderm*) is destined to give rise to the body musculature, including the walls of the blood vessels. Beneath the dorsal rudiment of the central nervous system a rod of tissue is detached from the roof of the primitive gut in the mid dorsal line. The cells of this rod later become vacuolated, and the structure constitutes a stiff skeletal axis, the *notochord*. Around the notochord, which is found in all Vertebrate embryos, the vertebral column is laid down at a later stage, and in land vertebrates the notochord is entirely replaced in later life by the solid axes of the vertebræ (centra, vide Chapter XI), but in fishes it persists to a greater or less extent throughout life.

Development of the chick and human being. The development both of the egg of the fowl and of the human being differs in one important respect from that of the frog. Segmentation in the fowl and in man leads to the formation of a number of membranes which enclose the embryo before birth, but are discharged at the end of the embryonic life. After fertilisation, the nucleus of a fowl's egg divides repeatedly, but as the yolk does not all divide with the nuclei, a thin plate of cells is demarcated on the surface of the yolk (Fig. 53). This plate of cells grows over the surface of the egg, and gives rise to a sac enclosing the yolk and to a series of envelopes which wrap round the embryo proper (Fig. 54). The remains of the yolk sac are often present at the time of hatching. The human egg cell has practically no yolk, and it develops at first into a hollow ball of cells like the egg of the frog, but only a part of this hollow sphere grows into the embryo properly speaking. Like the embryo fowl, the embryonic human being is invested with a series of envelopes. These envelopes, more especially the *allantois* (Figs. 54, 55), enter into very

close connection with the wall of the womb, which is specially well supplied with blood-vessels during the nine months

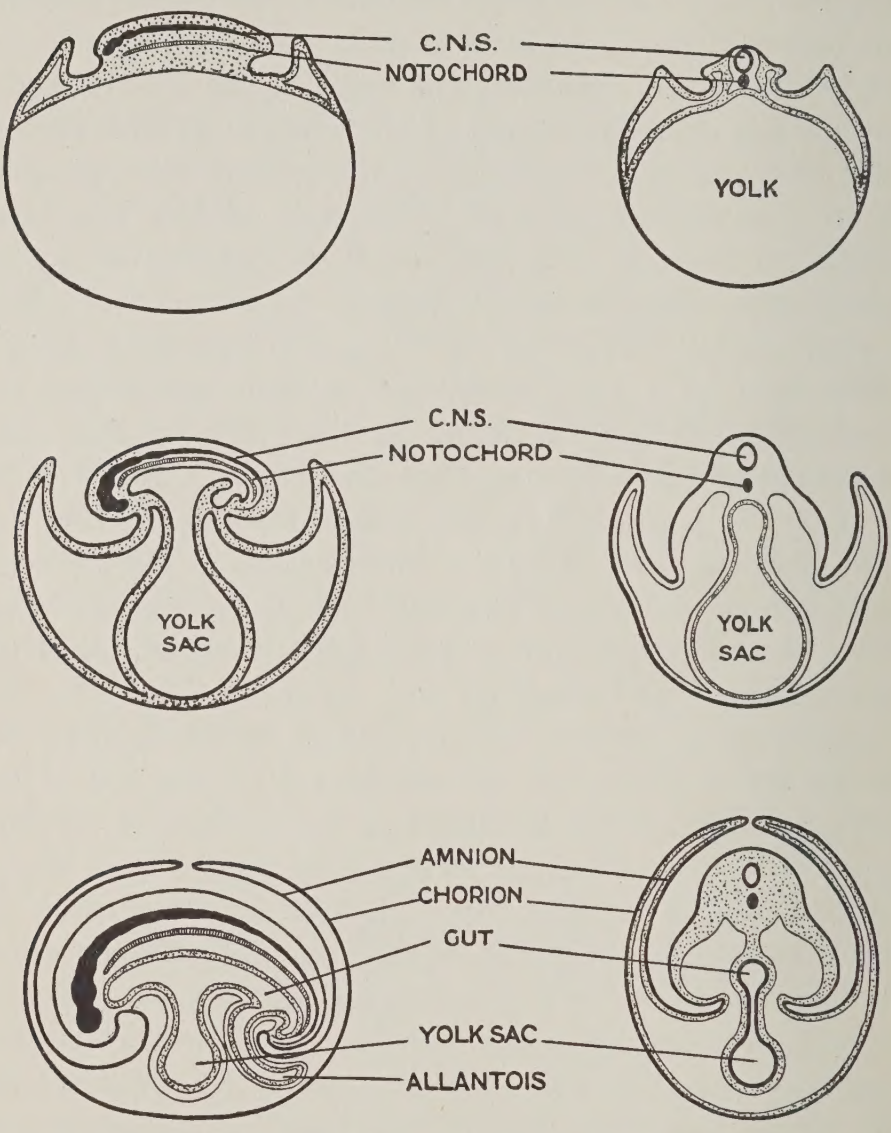

FIG. 54—FORMATION OF THE FOETAL MEMBRANES OF THE CHICK

On the left longitudinal, right transverse, sections with reference to the long axis. Top—at end of first day of incubation; middle—at end of the second; bottom—a later stage.

during which development completes itself within the body of the mother. By the diffusion of nutrient matter through the thin films of tissue which separate the blood

vessels of the mother from those of the embryo, the latter is able to grow in spite of the fact that the egg itself has no yolk.

Another feature common to the development of the fowl and the mammalian egg is the fact that, though terrestrial,

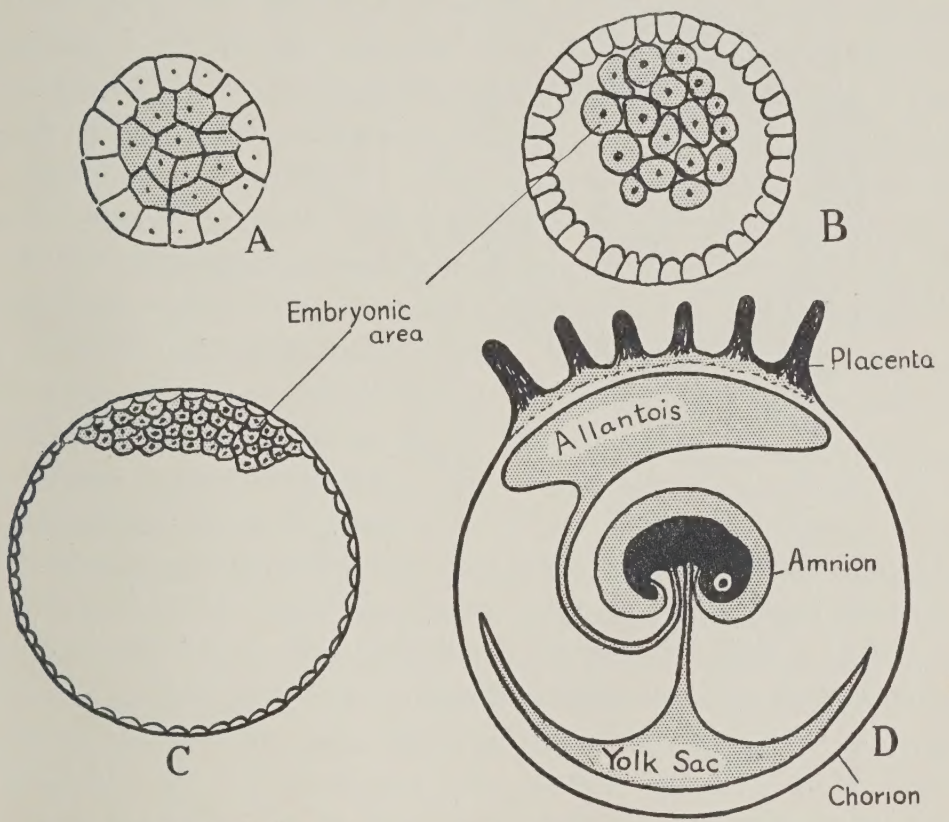

FIG. 55—THREE STAGES IN THE DEVELOPMENT OF THE MAMMAL

A, Early cleavage stage. B and C, Separation of the embryonic area. D, Foetus with its membranes.

the embryo at a certain stage has pharyngeal clefts, like those of tadpoles or fish; moreover, the heart is at first undivided longitudinally and gives off a series of symmetrical arterial arches.

Metamorphosis. After the embryo of the frog has reached the stage when the gut rudiment and the beginnings of the C.N.S. have been differentiated, it grows more rapidly in the axis parallel to the length of the spinal cord. After about a

fortnight the head and tail ends are distinguishable, the muscles of the latter are sufficiently active to enable the embryo to wriggle out of the mass of jelly in which the eggs are laid, and a new phase of independent existence starts. Unlike ourselves, however, the frog does not begin its separate existence with an organisation very much like the sexually mature form. In human beings the young organism at birth is essentially an immature adult. It is true that it has no teeth, and even after it acquires teeth it has to shed one set of them before the permanent set appear. In addition the sexual organs are immature and remain so until about the age of fourteen, when certain minor distinctions between the sexes (*secondary sexual characters*) such as the pitch of voice, presence of hair on the upper lip and chin of the male, and enlargement of the milk glands in the female, become evident. Otherwise a human adult is in most respects, anatomically speaking, a grown-up baby. But the embryo of the frog, which has hitherto grown at the expense of food or " yolk " stored in the egg, when it first starts independent feeding, is very different from the adult. It breathes like a fish by gills and not by lungs; and the arterial system is essentially fish-like. It has no fore limbs and only the tiniest rudiments of hind limbs. It possesses a tail.

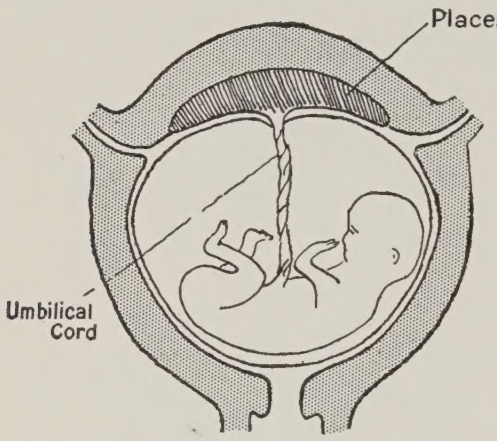

FIG. 56—THE HUMAN FOETUS IN UTERO SHOWING PLACENTA (above)

On each side of the throat in the newly hatched tadpole of the frog shortly after the time of hatching out there are four clefts which communicate with the exterior and with

the throat, thus enabling water to pass from the mouth outwards. The walls between these clefts are known as the gill arches. From the first three gill arches there grow out on either side tufts of filaments well supplied with blood vessels. These external gills, as they are called, disappear within a few days. The sides of the gill arches become invested with folds of skin very richly supplied with blood vessels like the gills of a fish. A fold of skin, the operculum, grows back over the gill clefts, as in many fishes, and conceals the gill from outside. The tadpole continues to breathe partly by its skin and partly by passing water over the gill clefts, which absorb the oxygen contained in it; and at first it has no true lungs. Apart from the fact that it has no true fins it is very much like a fish. This state of affairs is not permanent. The tadpole stage lasts only about three months in the case of the common European frog. An abrupt change supervenes; and in a very short time the adult characteristics are assumed. This change is spoken of as *metamorphosis;* and the preceding phase or tadpole stage is spoken of as the *larval period.* At metamorphosis the hind limbs, which in the half-grown tadpole are tiny rudiments, begin to grow rapidly; then the fore limbs break through the skin; finally the gill clefts begin to close up and the tail shrinks.

A four-legged, air-breathing, tailless adult is thus formed. The way in which an animal develops is a very difficult problem to understand and we are only just beginning to do so. A full discussion of the present state of our knowledge would take us too far afield. Nevertheless, it is well to realise that it is possible to experiment with the development of a frog or toad just as it is possible to experiment with the heart or the stomach (Fig. 57). We can make the eggs of a frog or toad grow up into individuals with two heads or two tails or with one eye on the top of the head instead of two (Fig. 58). There is, moreover, one question about the

development of the toad or frog which we are beginning to understand, and which is not too difficult to discuss at this stage, namely what brings about the sudden transformation from the tadpole into the adult form.

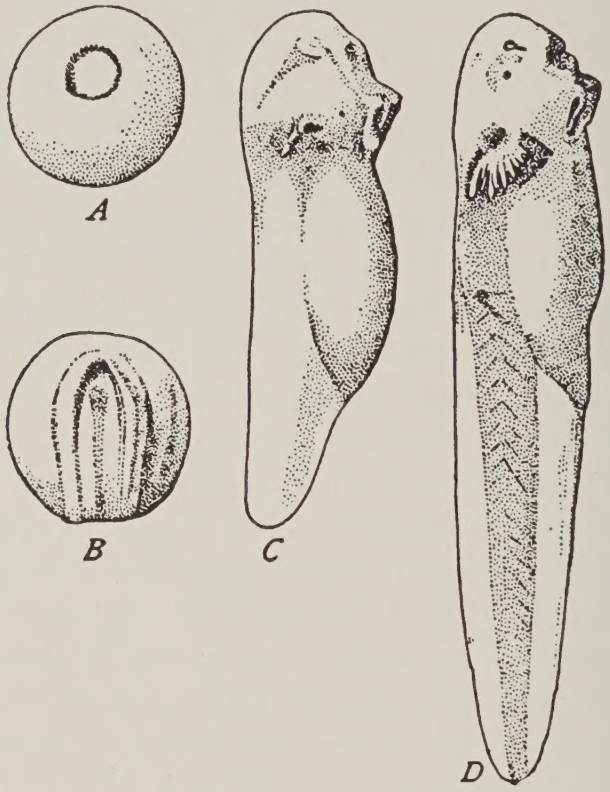

FIG. 57—EFFECT OF TEMPERATURE ON THE DEVELOPMENT OF THE FROG TADPOLE. (A) YOLK PLUG FORMED. (B) NEURAL FOLDS FORMED. (C) MAIN ORGAN-SYSTEMS FORMED. (D) READY TO HATCH, NOTE EXTERNAL GILLS. ALL THE EMBRYOS ARE THREE DAYS OLD; BUT THEY WERE KEPT AT 11°, 15°, 20° AND 24° RESPECTIVELY

There is in the neck of human beings a gland known as the *thyroid gland.* It is represented in the frog by a pair of glands on either side of two large veins of the neck region known as the external jugulars. In both man and the frog the thyroid gland consists of small capsules of a jellyish material and is very richly supplied with blood vessels (Fig. 49). Like the adrenal and pituitary glands it has no

duct and such organs are for that reason sometimes called ductless glands. The jellyish material of the thyroid gland is peculiar in that it contains a compound of iodine, an element not found in other tissues of the animal body. When the thyroid gland of any animal is given as food to young tadpoles they very rapidly start to develop limbs and to lose their tails. A large American frog, which normally lives for two years in the larval stage, will undergo metamorphosis within six weeks from hatching if fed on a thyroid diet. Now the thyroid gland can be removed by a

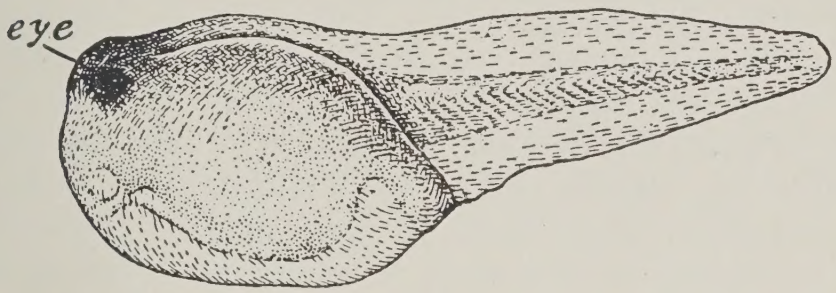

FIG. 58—ONE-EYED TADPOLE

Produced by exposing the yolk plug stage to the action of lithium chloride.

comparatively simple surgical operation about the time of hatching, and tadpoles that have been deprived of their thyroid glands, though otherwise normal, will go on growing for years without undergoing metamorphosis. In fact they never assume the adult characteristics. Incidentally it may be mentioned that there is among human beings a disease of infancy known as *cretinism* which is characterised by permanent undergrowth and persistence of childish characteristics. It can now be cured, as these cretin tadpoles can be cured, by giving thyroid gland (dried and in tabloid form) as medicine. We see from this that metamorphosis occurs when the thyroid gland begins to pour its secretion into the blood. Tadpoles can also be prevented from developing into the adult form if kept in water free

of any trace of iodine compounds. The thyroid is then unable to build up its secretion, which is an iodine compound. This compound can now be manufactured from pure chemicals in the laboratory. Allied to the frogs and the toads are the salamanders, in appearance somewhat like a lizard without scales, but having a larval stage spent in the water like the tadpole. The Mexican salamander in nature remains all its life and breeds in the larval condition. It is called by the natives "axolotl." The axolotl can be made to develop into a land-dwelling salamander after three weeks of feeding on thyroid gland (Fig. 59).

Heredity and Environment. This gives us the opportunity of examining two words used very loosely by people who have no biological training. The Mexican salamander does not develop into the land form in nature, because it *inherits* from its ancestors an inefficient thyroid gland. Tadpoles in the Swiss mountain lakes often fail to develop because there is insufficient iodine in their *environment.* By inheritance we simply mean the stuff which the sperm and the egg contribute to the new being. How that stuff will shape depends partly on what sort of stuff it is, that is to say on what sort of parents it came from; and partly on the surroundings in which it finds itself. Before the nature of reproduction was understood, as we understand it to-day, it was generally believed that any bodily change which results from a change in our surroundings can be transmitted to our children. This view was stated in a very explicit form by Lamarck in his *Philosophie Zoologique.* Experiment does not support this belief. The hereditary stuff does occasionally undergo great changes—sports appear, and breed true to their new characteristics; but otherwise the same materials are transmitted from generation to generation unchanged through the sperm and the egg. Heredity and environment are different aspects of development; but they are independent of one another: what we inherit is a

capacity to develop in a particular way in a particular environment.

Two authors have recently expressed this distinction very clearly in the following passage :—

Many plants grow both high up among mountains and down in the plains and valleys. Those which grow higher up must exist in lower temperature, longer winter, more violent weather, poorer soil. As a result, they grow into a shape quite unlike that of the lowland variety. The Dandelion, for instance, when growing in the Alps is a dense rosette of small leaves, a long root, and a short flower stalk ; in the lowlands, as we all know, its stalk may be long, its leaves large and spreading, its root (though too long for the gardener) much shorter. If dandelions from the Alps are taken down and grown in the plain, all their new growth is of lowland type, and in a short time they become indistinguishable from lowland dandelions, while exactly the reverse is true of lowland plants transplanted to the Alps. The same is true when seeds of the Alpine type are sown in the plains, and vice versa. The time spent in an Alpine environment has not in the least fixed the Alpine habit of growth.

This can be readily understood if we suppose that the Dandelion has a fixed constitution which, however, reacts differently to different external circumstances ; it has, that is to say, a fixed capacity of being modified in special ways. This is obviously true for simple chemical substances. One particular sort of paraffin, for instance, melts at, say 61°, another at 62° C. Keep the former in one environment—below 61°—and it stays solid ; keep it above 62°, and it stays liquid. But you will not make it raise its melting-point however long you keep it melted. The two will continue to show their characteristic modifications in relation to heat—their original melting-points—as long as you like to keep them. To take another example, this time from the animal kingdom, attempts have been made to explain the black colour of the negro as the accumulated effect of generations of sun-burn. It is of course true that most white men in a tropical climate become sun-burnt ; the strong sunlight has a direct effect on causing more pigment to form in the skin. But anybody can verify for themselves the fact that the children of men tanned in this way are not noticeably less white than those of parents who have never left England.

What does this imply? Surely, that European and negro have different constitutions as regards skin-colour. The European stays pale in temperate countries, darkens in the tropics. But the negro is black wherever he lives. We can go back to our previous comparison; we can think of two grades of paraffin, one melting at 65° C., and the other at 40° C. The first, if kept in the shade, will remain solid throughout the summer in any region of the earth; but the other, though it would stay solid in an English summer, would be liquid in the tropics.

This interpretation would clearly leave no room for the Lamarckian theory, and, as time has gone on, more and more of the examples that Lamarckians claimed as proving their point have been shown to be explicable in some such way as this.[1]

When the Lamarckian principle was first challenged, prominent scientists, like Cope, were willing to come forward and state that a certain cock deprived of one eye transmitted eye-defects to all his offspring. When it was conclusively proved that mutilations effected through several generations left no impress on the hereditable characters of the stock, the Lamarckians fell back on the gratuitous postulate that only "adaptive" changes could be transmitted. The precise meaning of this adjective was never defined, nor was any reason forthcoming to suggest the existence of a mechanism that could discriminate between mutilations and bodily changes that are "adaptive." The "Neo-Lamarckian" view, that acquired characters gradually become impressed on the hereditary constitution only after countless generations, transfers the issue from the plane of verifiable experience to one of pure surmise, rendering further discussion meaningless. On one point we can be quite definite. If the Lamarckian idea is true there must be some mechanism by which the tissues of the body can influence the germ cells in a *specific* fashion. Experiments exist which throw light on the question, such as the work of Castle and Phillips (1909–11). If the ovaries of an albino guinea-pig are removed from the body and

[1] J. B. S. Haldane and J. S. Huxley—*Animal Biology.*

FIG. 59—ON THE RIGHT, AXOLOTL LARVA OF MEXICAN SALAMANDER. ON THE LEFT, SAME SIX WEEKS AFTER FEEDING WITH THYROID GLAND—IT HAS NOW ASSUMED THE ADULT FORM

replaced by ovarian tissue from a black female of pure stock, the offspring produced when the ingrafted female is mated to an albino male are all black, without white hairs, as they would be in the case of a black female crossed to a white male. They are in fact indistinguishable from the offspring of a normal cross between a black and albino guinea pig.

In attempting to understand the tenacity with which the belief in the Lamarckian principle has clung to biological thought, it must be borne in mind that embryology is the most recently developed branch of anatomical science. The prevailing idea about development until the classical researches of von Baer and Meckel in the first half of the nineteenth century was that each organism was from the very first complete in all its parts and only needed growth to make its minute structure manifest to the eye. Caspar Wolff, in 1759, made observations on the hen's egg that led him to enunciate the "epigenetic" as opposed to the prevailing "evolutionary" view. That is to say, he sought to show that the hen's egg is at the beginning without any gross anatomical organisation and that structural organisation within the egg is a gradual development. His work was disregarded entirely at the time. Von Baer's researches on the same subject were published synchronously with the formulation of the Cell doctrine (1832). We may thus say that until the middle of the nineteenth century, the current conception of inheritance in biology was closely analogous to the legal notion. The parent was supposed to hand on its characters to the offspring in the same sense as the well-to-do hand on their belongings. With so erroneous a conception of the nature of development to guide them, it is little wonder that the idea of the inheritance of acquired characters seemed a perfectly reasonable one. Nor is it any cause for surprise that the doctrine of Lamarck should have been first called in question during the decade that

first saw a clear recognition of the nature of fertilisation and the process of maturation in the germ cells.

Side by side with the citation from Haldane and Huxley given above, may be quoted the following passage from Goodrich (1924), who expresses the same conclusions with admirable lucidity :—

> Owing to that universal property of irritability or the power of response to stimuli already described, all organisms are the result of the interaction of the factors of inheritance, and the conditions of the environment. By the latter we mean all those conditions or stimuli which are capable of influencing the differentiation, growth, behaviour or, in other words, the metabolism of the organism. By the factors of inheritance, on the contrary, we mean that complex association (transmitted from the parents) of substances with properties or capacities which make up the specific inheritance characteristic of each organism, and which may be called its assemblage of germinal factors of inheritance, or its germinal constitution. They are contained in the germ-plasm, and constitute the physical basis of inheritance. Not only are organisms as we see them before us necessarily the results of the combined action of these factors and conditions, but so also is every part of them, every structure, every activity, every organ, every habit. Therefore the characters observed and measured, dealt with in statistics and experiments, are likewise their products. The inheritance might be compared to a musical instrument, the stimuli to the player, and the organism and its characters to the music produced. What particular tune is called forth will depend on the player, but the range of possible sound will be limited by the structure of the instrument, by the factors which make up its capacity to respond to the touch of the player.
>
> Every character of whatever kind is, in a sense, partly acquired, since it is called forth by stimuli, and partly inherited, being a product of the activities of the germ-plasm ; and no character is more acquired or more inherited than any other. Hence the popular distinction between acquired and not acquired characters, between those which have been developed in the course of the individual's lifetime and those which are inborn, is misleading. The very terms involve a fallacy. We cannot point to this or that bodily or mental structure and say this is acquired and that

is not. Characters being of the nature of a response must necessarily be produced anew at every generation. The characters of an organism are but the sum of its past responses.

Sir Ray Lankester (1894) drew attention to the important fact that characters are responses, and pointed out that Lamarck's first law, that a new stimulus alters the characters of an organism, contradicts his second law that the effects of previous stimuli are "fixed" by inheritance. The Lamarckian position is illogical, and to support it its advocates are driven to the performance of "illogical" experiments. They usually begin by taking an organism and submitting it to a new stimulus. If a change is thus induced, this very fact shows that the previous stimulus (under whose influence the organism has perhaps been living for centuries) has not "fixed" the character in inheritance. To prove that characters are rendered permanent, evidence is constantly brought forward that they are changeable.

Only those characters reappear regularly in successive generations which depend for their development on stimuli always present in the normal environment. Others, depending on a new or occasional stimulus, do not reappear in the next generation unless the stimulus is present. But both being equally due to factors of inheritance and to conditions of environment, the popular distinction between acquired and not acquired characters is illusory. In every case it is the material basis with the capacity to acquire, to become modified, or to respond, which is really transmitted; the direction and extent of the response depends on the stimulus encountered. The presence of a given hereditary factor cannot be determined by mere inspection of the characters of an organism; the factor may be present, but the corresponding character fails to show itself owing to the absence of the necessary stimulus. On the other hand, dissimilar stimuli acting on different factors may give apparently similar results. "*Heredity*" must be admitted to include two different processes—the transmission of the factors of inheritance, and the reappearance of characters in successive generations. To avoid confusion we speak of the factors as transmitted and the characters as inherited. It would be well to drop altogether the use of the expression "acquired character." Confusion would be avoided if we adopted the clear system of nomenclature proposed by Professor W. Johannsen, and much used in America. He uses the term "gene" for a factor, "genotype" for the whole assemblage of factors transmitted from one generation to the next, and

" phenotype " for the characters developed from them in a particular environment. Thus, one genotype may give rise to a number of different phenotypes, according as the environment is changed. Modifications, then, are not transmitted as such. In the absence of the stimuli which originally gave rise to them they could only reappear if the new environment produced such a change in the factors of inheritance themselves that, when replaced in the old environment, they continued to respond as if the new stimuli were still present. This is what the Lamarckian theory of evolution demands. We will not say that such a thing is impossible, but it is in the highest degree improbable, and it is very difficult to conceive how such a result could be reached. At all events, no case of the supposed transmission of modifications has yet been brought forward which could not be better explained in other ways.[1]

The Sexual Metamorphosis. One question of special interest to ourselves may now be mentioned. About the age of twelve to seventeen there is more or less abrupt development of what we have already called the " secondary sexual characters " in girls and boys. The age of *puberty* may be compared to the period of metamorphosis in the frog. At puberty, so-called because of the appearance of hair on the pubic region (*i.e.* the region where the legs join the trunk), the ovaries begin to liberate egg cells and the testes begin to manufacture seminal fluid.

The development of the secondary sexual characters, *e.g.* bass voice and beard of the male, can be prevented by removal of the gonads, just as the metamorphosis of the toad can be prevented by removal of the thyroid glands. One result of removal of the gonads (castration) is that the individual tends to deposit fat in the tissues, for which reason castration is practised in agriculture, where a single normal male suffices to serve a large number of females. From ancient times castration was practised on the male human subject. Such individuals are called eunuchs.

The assumption of the most obvious differences between

[1] *Living Organisms*—Oxford University Press.

the sexes is correlated with the activity of the gonads in many animals, just as the loss of the larval characters is dependent on the activity of the thyroid gland in frogs, toads and salamanders. In fowls the hen will assume the plumage and spurs of the cock, if the ovary is removed at any time in the life cycle. Male crabs attacked by the parasite *Sacculina*, develop the characteristic female configuration of the abdomen and pincers, when their testes are destroyed by the parasite. We are thus led to enquire into the factors which, in the course of development, determine whether a male or female type of gonad will be formed.

There are a number of facts about animals which suggest the intervention of some agencies tending to predetermine the sex of the developing organism at a very early stage in development, in fact at the time of fertilisation. Thus to mention a familiar one, we know that the male bee or wasp is produced from unfertilised eggs, the female being produced in the usual way. This is true of the entire order of insects (Hymenoptera) in which bees and wasps are placed, and also of the minute freshwater wheel animalcules (Rotifera). In some animals the products of the first segmentation divisions separate, and several embryos are produced from one egg. When this happens, as in the production of "identical twins" in the human species, the individuals produced from a single egg are always of the same sex. The nine-banded armadillo produces litters of four or five young from a single egg. Individuals of the same brood are in this case always of the same sex, but in related species of armadillos, in which *polyembryony* does not occur, individuals of the same litter may be either male or female. Clearly something which happens before segmentation begins is here the important factor, and we are thus led to probe more deeply into the process of fertilisation and the nature of cell division.

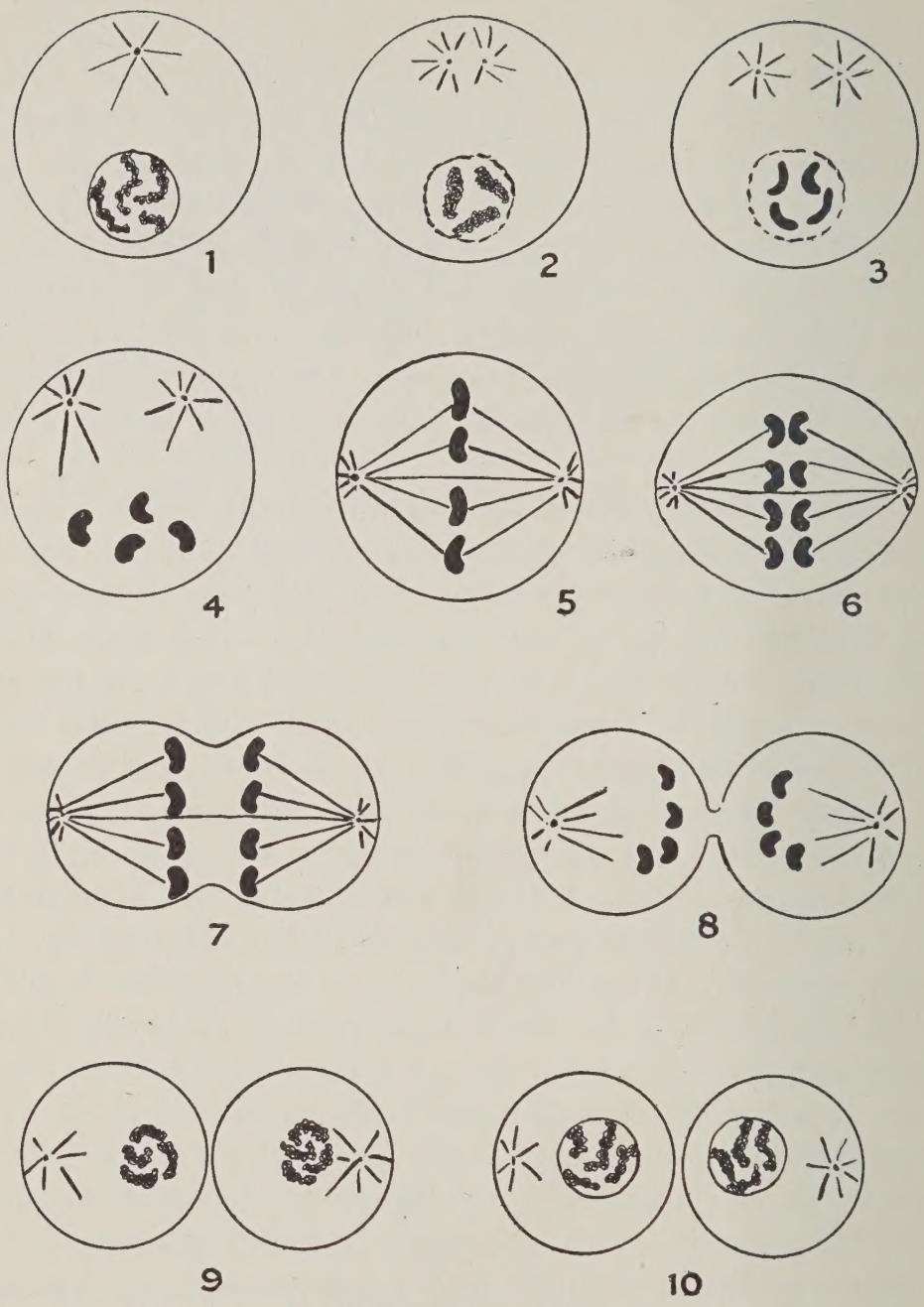

FIG. 60—DIAGRAMMATIC REPRESENTATION OF NUCLEAR DIVISION IN A SPECIES WITH FOUR SIMILAR CHROMOSOMES

Nuclear Division. Nuclei of resting cells appear in microscopic preparations as vesicles containing a tangle of finely-spun threads. At one side of the nucleus is a small area in the cytoplasm, the *attraction sphere*, whose separation into two parts heralds the inception of cell

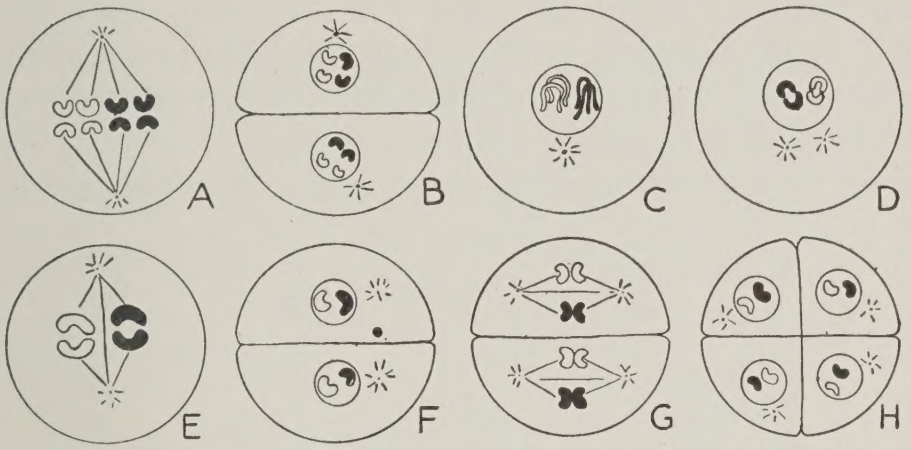

FIG. 61—REDUCTION DIVISIONS IN MALE OF A SPECIES WITH FOUR SIMILAR CHROMOSOMES, AS IN FIG. 60

A, Normal division. E, Reduction division.

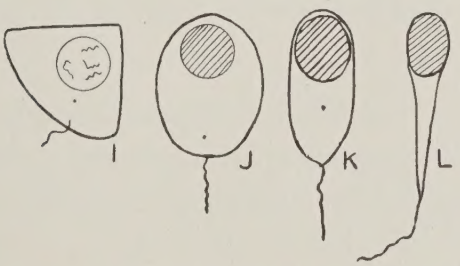

FIG. 62—CONTINUATION OF FIG. 61

Showing transformation of a reduced cell of the testis into a sperm.

division. As the two attraction spheres separate they appear to draw out the surrounding cytoplasm into a *spindle* of fine fibrils. Meanwhile, changes have taken place in the nucleus itself. The tangle of fine threads has resolved itself into a number of readily distinguishable filaments which become progressively shorter, assuming

the appearance of stout rods or blocks staining deeply with basic dyes. These rods are known as the *chromosomes* (Figs. 60–64). They arrange themselves on the equator of the spindle and split longitudinally in halves. The halves pass to opposite ends of the spindle, and while the division of the cytoplasm completes itself, they spin out again into fine threads, from which the nuclei of the daughter cells are built up. Thus each of the chromosomes in the nucleus of any cell is structurally equivalent to a corresponding chromosome in that of the preceding and succeeding cell generations. In every species

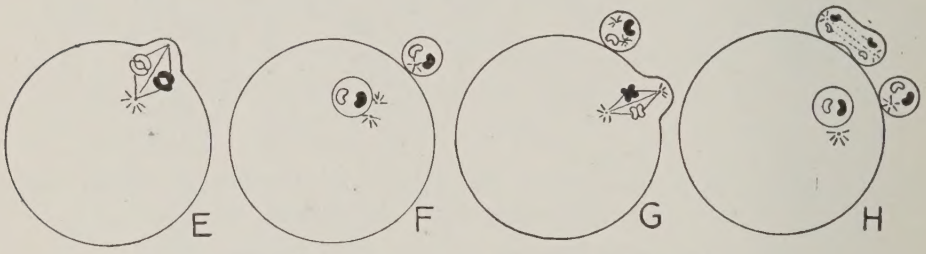

FIG. 63—REDUCTION IN THE FEMALE

The antecedent stages correspond to stages A–D in Fig. 61.

of organism the number of chromosomes which can be counted in dividing nuclei is constant, and the elaborate method just described by which nuclei divide (*mitosis*) ensures the maintenance of this constancy.

The important fact that the nuclei of any one species of animals form into a constant number of chromosomes when the cells divide was established during the seventies by Flemming, Strasburger, Butschli and other workers. But with this discovery a new problem arose. During fertilisation, as we have seen (Fig. 3), the nucleus of the sperm unites with that of the egg to form a single nucleus of compound origin. Why does this not result in a doubling of the number of chromosomes in the nucleus? What ensures that each

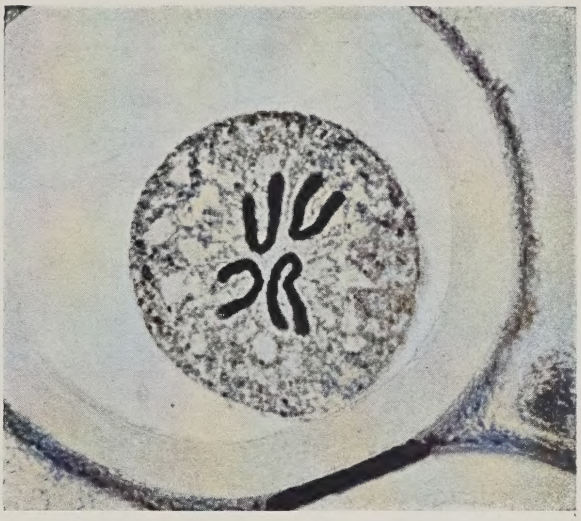

FIG. 64—MICROPHOTOGRAPH OF A DIVIDING CELL, IN STAGE 5 OF FIG. 60, SHOWING FOUR U-SHAPED CHROMOSOMES

generation has the same chromosome number as the last?

As already stated (p. 18), the formation of ripe sperms or eggs is the final stage of a long process of repeated cell-division within the testes or ovaries. Now all of these divisions except one take place in the manner already described. But the last division but one before the formation of the actual ripe gametes is peculiar (Figs. 61, 62, 63). Just before this division, the chromosomes come to lie side by side in pairs—a process known as *synapsis*—and during the subsequent division, when the stage corresponding to 5 of Fig. 60 is reached, it is these pairs which lie on the spindle. Instead of the chromosomes splitting in halves, as is normally the case, the pairs now part company, and one member of each pair goes into each of the daughter cells. So each of the resulting cells, and therefore (as the next division is perfectly normal) each of the gametes, has exactly half the number of chromosomes characteristic of the species. At fertilisation the normal number is of course restored; and the important conclusion follows that every ordinary cell of an individual organism has a chromosome set of which half the components are paternal in origin and half maternal.

Reduction. In both sexes the *reduction division*, as this exceptional division of the nucleus is termed, occurs in the same way. In the male it is followed by division of the rest of the cell, and each daughter-cell divides again in the normal manner, so that four sperms, each with half the typical chromosome number, result (Figs. 61, 62). But in the female, although the nucleus divides twice, just as it does in the male, the rest of the cell does not divide. One only of the four resulting nuclei is retained within the egg-cell; the other three are extruded and degenerate, constituting the so-called *polar-bodies* (Fig. 63). The significance of this difference is not clear.

Now, in many animals and plants it is possible to distinguish, among the chromosomes, pairs of different sizes

and shapes—this is the case, for instance, in the fruit-fly *Drosophila*—and it is possible to see that each gamete receives one representative of each pair.

This fact has proved to be of first-rate significance in the search for a material basis for the interpretation of experiments upon inheritance. Consider as a concrete illustration, the case of the stone-fly *Perla*, as described by Nakahara (1919). In the unripe germ cells of the male (Fig. 65) the chromosome complex consists of ten elements differing *inter se* in the following way: one pair, $\alpha\alpha^1$ are rod-like and equal, two pairs, $\beta\beta^1$ and $\gamma\gamma^1$ are V-shaped and equal, one pair, $\delta\delta^1$ are much smaller and spherical in contour, the fifth pair being composed of unequal rods X and Y, whose special significance will become clear at a later stage. After reduction the sperms contain five chromosomes, viz.: α or α^1, β or β^1, γ or γ^1, δ or δ^1, X, or Y. Similarly the female gamete will contribute one member of each pair to the fertilised egg, which hence possesses five pairs of chromosomes like its parent. The nucleus of the fertilised egg divides so that the daughter nuclei of the first cleavage receive a representative of each of the chromosomes. Cell divisions follow in rapid succession during the up-building of the embryo. Thus each cell of the individual contains five pairs of chromosomes, one member of each pair derived from the father and the other from the mother. As the result of reduction each gamete receives one component of each pair, that is to say, with respect to each

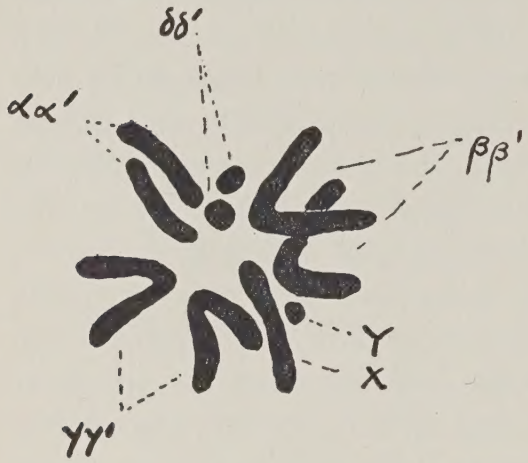

FIG. 65—CHROMOSOMES OF THE STONE-FLY

pair of chromosomes the formation of the gametes involves the *segregation* of its paternal and maternal components.

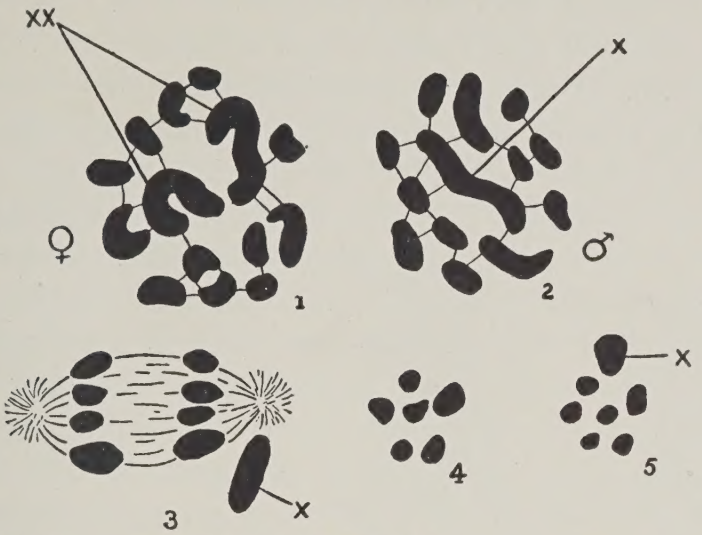

FIG. 66—CHROMOSOMES OF THE PLANT BUG PROTENOR

1, of female; 2, of male; 3, the reduction division in the male (see E of Fig. 61); 4, male-determining and 5, female-determining sperms, resulting from the unequal division in 3.

The principle of segregation we shall find later to be of the utmost significance in studying hereditary transmission.

The Determination of Sex. In the stone-fly, there is

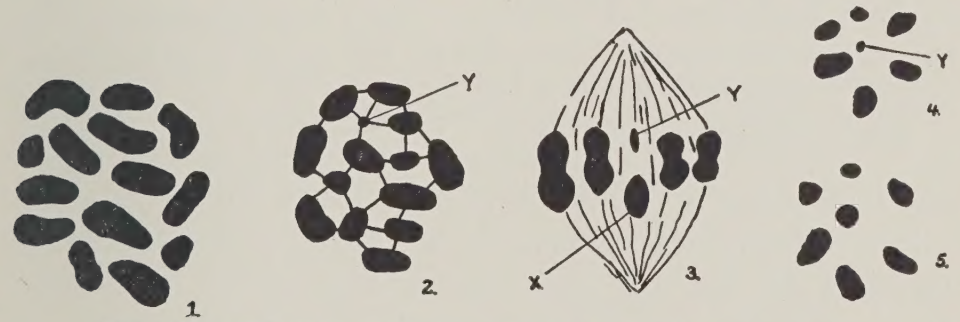

FIG. 67—CHROMOSOMES OF THE PLANT BUG EUCHISTUS

Numbers as in Fig. 66.

another feature which calls for further comment. This is the existence, as in many animals, of one unequally mated pair of chromosomes, the XY pair. When this occurs, it occurs in one sex only; in the alternative sex there is a corresponding equal pair (XX). In birds

and Lepidoptera (butterflies and moths), the female is the XY, the male the XX individual. In other animals the male is usually found with sufficiently careful measurement to have an unequal (XY) pair which is equally mated in the female (XX). During the nineties some animals were found that had in one sex an odd number of chromosomes: this at first sight seemed to conflict with the numerical constancy of the chromosomes. In the early years of the present century the American zoologists provided the key to an understanding of the discrepancy. In all such cases the alternate sex has one more chromosome. Take the case of the large cockroach which haunts our bakehouses. The male of *Periplaneta americana* (its technical name) has 33, the female 34 chromosomes. The eggs all have 17 chromosomes, one half of the sperm have 17, the other half 16 chromosomes. (Compare Figs. 66, 67). If a sperm of the former class fertilises an egg, the individual produced will be a female (17 + 17 = 34), and if a sperm of the second type fertilises an egg, the individual produced will be a male (17 + 16 = 33).

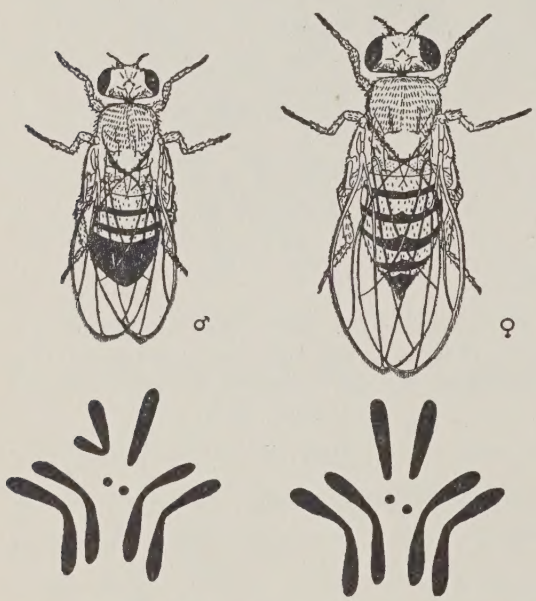

FIG. 68—THE MALE (left) AND FEMALE (right) OF THE BANANA FLY (DROSOPHILA MELANOGASTER) AND THEIR CHROMOSOMES

Similarly with the XY chromosomes. The male of the human species has 23 equal pairs and 1 unequal pair (XY) of chromosomes in the unreduced nuclei. Thus two types of sperm are produced, X-bearing and Y-bearing respectively, the one female producing, the other male

producing. The modern theory of sex determination fits in well with many biological facts, and is confirmed by two independent lines of evidence, one of which will be discussed at length later. The other may be mentioned here. In species having an XY pair in the male, measurement of the sperm heads shows two distinct modal values around which the observations group. This suggests the possibility that by gravitational or other methods it may be possible eventually to separate seminal fluid into portions containing predominantly one or other type of sperm, the X-bearing or Y-bearing. If this could be done the control of the sex ratio would be experimentally realisable.

Many medical men still adhere to the superstition that the sex of human offspring depends upon whether the egg fertilised is derived from the right or left ovary. Apart from the very conclusive evidence we have from other sources that this view is wrong, it is demonstrably false in other mammals, where removal of the ovary of one side does not affect the sex ratio. In this connection, one may pertinently recall the words of Sir Thomas Browne :—

> And therefore what admission we owe unto many conceptions concerning right and left requireth circumspection. That is how far we ought to rely on the remedy in Kiranides, that is the left eye of a hedgehog fried in oil to procure sleep, and the right foot of a frog in a deer's skin for gout ; or that to dream of the loss of right or left tooth presageth the death of male or female kindred, according to the doctrine of Artemidorus. What verity there is in that numeral conceit in the lateral division of man by even and odd, ascribing the odd unto the right side and even unto the left ; and so, by parity or imparity of letters in men's names to determine misfortunes on either side of their bodies, by which account in Greek numeration Hephæstus or Vulcan was lame in the right foot, and Annibal lost his right eye. And lastly what substance there is in that auspicial principle and fundamental doctrine of ariolation, that the left hand is ominous and that good things do pass sinistrously upon us, because the left hand of man respected the right hand of the gods, which handed their favours unto us.—(*Vulgar Errors.*)

When the sex chromosomes were first discovered the conclusions we have outlined seemed to conflict with the well-known fact that many familiar animals change their sex under certain conditions. But we may presume that whatever influence the X chromosome exerts requires the proper co-operation of external agencies ; indeed the facts of sex transformation fit in very well with the hypothesis, now they have been studied more carefully. Crew found (1921) that, whereas the offspring of a normal mating in frogs produces the customary 1 : 1 ratio of male and female offspring, a quite different result occurs when we mate with a normal female a male that started its life as a female. He reared a generation of seven hundred offspring of such a cross, all females. If the transformed male was, as its former life would suggest, an XX individual in disguise, it could produce no Y-bearing sperm and therefore no male offspring.

Chapter VII

THE MACHINERY OF INHERITANCE

IN the last chapter we have studied the characteristic features of the development of a new being, and in so doing we have dwelt on the fact that the external conditions under which the fertilised egg develops have a very important influence. Thus we have been led to make a distinction between two aspects of the question of development, the nature of the conditions which affect the segmenting egg and growing embryo, and also the kind of materials which the sperm and egg respectively contribute to the constitution of the new organism at the time of fertilisation. Now it is a matter of common knowledge that the fertilised egg of one species of animal, if allowed to develop under the same conditions as the fertilised egg of another species, will not lead to the production of the latter type of adult. It is a universal experience that any dog resembles its father and mother in more respects than it resembles any cat or any fish ; any cat resembles its father and mother in more respects than it resembles any dog or any fish ; any fish resembles its father and mother more closely than it resembles any cat or any dog. We may express this by saying that cats, dogs and fish have certain specific hereditable properties. If we examine these hereditable properties we find that a cat has more hereditable properties in common with any dog than those which it shares with any fish. Thus organisms can be arranged or classified in groups

expressing the extent of resemblance in their hereditable properties.

The Problem of Inheritance. Within the limits of a single species, the differences exhibited by different individuals are not entirely due to differences of upbringing. We know that pure-bred White Leghorns separated by nothing more substantial than a thin partition of wire netting from a pen of pure-bred Buff Orpingtons will have offspring that are like their parents and not like the offspring of Buff Orpingtons. We know, too, that we can predict with certainty the characteristics of the offspring of a "pure-bred" strain of White Leghorns, but we cannot predict with the same precision the characteristics of the offspring of a mixed pen of poultry. Thus there arises a new sort of problem, namely to foretell how the characteristics of the parents affect the type of offspring produced, when the conditions of development are constant but the characteristics of the parents are different. This is the central problem of inheritance, the study of which is sometimes called *Genetics*.

The issue we have just stated is very much like another problem in science that has a somewhat similar history. It is like the problem of how two chemical reagents react together to form a new compound, and how the original constituents can be recovered when the new compound is in turn decomposed. Modern chemistry begins with the recognition of the principle of conservation of matter and the discovery by Richter (1792) of the law of constant proportions. Richter's discovery led Dalton (1802) to the atomic theory of matter, which leads us to a space-time picture of the mechanism of chemical reaction. We are still far from understanding the physical chemistry of inheritance, but we are to-day in a position to form a space-time picture of the process of combination of hereditable properties which takes place when a new unit of living matter is brought into being. Since the study of inheritance is to-day an

exact science, we shall devote some detailed consideration to it in the present chapter. Our first task will be to show that in the field of genetics, there is also a law of conservation of materials and a law of constant proportions, and that these two laws can be generalised in a Principle of Segregation which is closely analogous to the Atomic Principle.

As in the study of chemistry, we must start off with pure materials, that is stocks whose offspring we can predict, if the conditions are defined. Suppose we take a cock of the white variety of the Andalusian breed of poultry and a hen of the black variety—both individuals being selected from stocks which have been inbred for their characteristic plumage colour for a large number of generations, and are therefore, genetically speaking, pure materials. When these two individuals are mated their progeny will be found to be neither white nor black but intermediate between them, being slate-blue birds with feathers shading into blue-black upon the neck and back. If these blue hybrids are mated with one another their offspring will be of three kinds—white, black and blue—and if sufficiently large numbers of eggs are hatched the proportions will approximate to the ratio 1 : 1 : 2. Exactly similar results would follow if in the first place a black Andalusian cock had been mated to a white hen. We see from this, first, that the sperm and egg, though so different in size, contribute equally to the constitution of the fertilised egg ; second, that though the hereditable properties of both the parents seemingly disappear in the individual resulting from the combination of a particular sperm and a particular egg, they are really there but somehow hidden ; thirdly, that when the parental contributions reappear they do so in definite numerical proportions.

Mendel's Hypothesis. These conclusions were proved true of animals at the beginning of the present century, but they were discovered to hold good in plants nearly half a century

earlier by an Austrian Abbot, Mendel (1858–65), contemporary with Darwin. Mendel first formulated the Principle of Segregation which stands in the field of genetics for the Atomic Theory in chemistry. The experimental fact which Mendel discovered was that, when plants of different pure stocks are crossed and the offspring mated *inter se*, the pure parental types reappear in definite numerical proportions in the second crossbred generation. Mendel argued that,

(*a*) since the two parents contribute equally to the hereditary constitution of the offspring, and

(*b*) since there is no reason to suppose that the chance of any kind of gamete fertilising any other kind (of the opposite sex) is influenced by anything but the numerical proportions in which they are produced,

all the quantitative results could be shown to follow from the laws of chance, on the hypothesis that there are definite units of hereditary combination, contributed by both parents, and so distributed among the gametes that any particular gamete contains one member—either the paternal or the maternal—of a corresponding pair of units. These units are spoken of by Mendel as *factors*.

In the last chapter we have acquainted ourselves with material entities in the sperm and egg which do behave like Mendel's units, and the student will find it more easy to envisage what is implied by the Principle of Segregation, when we have seen how the behaviour of the chromosomes bears on the interpretation of such experiments as we have last described. But for the sake of historical perspective we shall insert a brief account of Mendel's own researches. The student may find it helpful to return to this after gaining the clearer insight which a study of the chromosomes affords us.

Mendel's hypothesis was greatly in advance of his time; his doctrine not only assumed the principle of fertilisation,

not then firmly established, but postulated the existence of material entities for which at that time no microscopic evidence was available. He worked long before the facts of mitosis and reduction, set forth in Chapter VI, began to be understood. When, in the opening years of the twentieth century, three Continental workers, de Vries, Correns and Tschermak, independently rediscovered his principles and unearthed his papers in an obscure horticultural journal, a knowledge of the microscopic bodies known as the chromosomes was already sufficient to confirm his conclusions, though derived from an entirely independent source.

Previous to Darwin's time various observations, which the reader will find recorded in *Variations of Animals and Plants under Domestication*, had been made on the crossing of different races (" species " or " varieties ") of plants and animals. Such experiments date from the work of horticulturists in the middle of the seventeenth century. Conspicuous success did not crown these early efforts, partly because the relation of parent to offspring was imperfectly realised, partly, again, owing to the fact that the pioneers in hybridisation tended to take the individual as a whole for their experimental unit. It is the essence of Mendel's own method that it deals with pure-breeding stocks differing only in well-defined particulars, employing single characteristics as units of study, and recording the progeny of every cross separately for comparative observation. In his original work Mendel chiefly employed the common pea. This possesses two advantages which recommend it for such experimentation, namely, that its flowers are capable of self-fertilisation (*i.e.* the pistil can be pollinated from the stamens of the same flower) and that it has a number of well-marked varieties distinguished by tangible characteristics such as the shape (round or wrinkled) and colour (green or yellow) of the seeds, or the stature (tall or dwarf) of the shoot, etc. A single example will

illustrate the fundamental genetic principle which Mendel discovered.

As a type of Mendelian experiment we shall consider the results of crossing a variety of pea having a dwarf shoot, from a stock breeding true to this feature, with an individual from another variety characterised by tall shoot, likewise of pure pedigree. When pollen from flowers of the one is transferred to the stigma of the other, the same result always occurs; every seed produced in consequence of such a union gives rise to a tall plant, whichever way the cross is made with respect to the sex of the parents. But if these seeds are allowed to germinate and grow into plants, the results of self-fertilising the flowers of the first generation (technically the F.1 or first filial generation of the cross), or, alternatively, crossing them with other F.1 plants, is entirely different from the effect of crossing two of the parental pedigree tall plants. Instead of obtaining only tall plants true to type, it is found that three-quarters of the seed produced (F.2 generation) give rise to tall plants, but one-quarter to dwarfs like one of the original parents. Further breeding shows that two-thirds of the F.2 tall individuals breed in the same way, throwing dwarfs in the same ratio; but that the remainder breed true to type like the original tall parent when self-fertilised, as do the dwarfs of the F.2 generation, which, when self-fertilised, or crossed *inter se*, have only dwarf offspring.

In endeavouring to interpret these observations we must recognise that the hereditary constitution of the tall individual in the F.1 generation differs from that of the tall parents, since they are capable of giving rise to dwarf offspring. It differs presumably in producing gametes characterised by the possession of some material (Mendel called it, without discussing its nature, a factor) responsible for the production of the dwarf condition. We notice also that in the F.2 generation the proportions of pure tall and pure dwarf plants are

identical, that is to say, one-quarter have the factor for tallness only and one-quarter the factor for dwarfness only, so that neither of the gametes from which an individual of either type originates contains the alternate factor. Furthermore we must bear in mind that the F.1 tall plants behave in a similar manner whether the factor for dwarfness is borne by the maternal or paternal gametes (ovules and pollen grains). Let us postulate that each F.1 tall plant produces in equal quantities gametes bearing the tall and dwarf factors respectively—but never both—and further that there is an equal chance of any pollen grain fertilising an ovule with the same or an alternative factor to that which it bears. It follows that the number of individuals produced in the F.2 generation containing both factors for the tall and dwarf conditions will be twice the number containing only the tall or only the dwarf factor. For T may fertilise T or D, giving TT or DT ; and D may fertilise D or T, giving DD or DT. This, of course, satisfies the conditions, and is an adequate account of the facts so far. It constitutes the hypothesis of Mendel, which states that characters distinguishing different hereditary strains depend upon factors which are inherited from both parents and *segregate* in the formation of the gametes, so that one-half contain the paternal and one-half the maternal factor.

The assumptions advanced may not involve every conceivable possibility, and the truth of the factorial hypothesis must stand or fall, like all other hypotheses, with its capacity to yield verifiable consequences. Consequences of a verifiable nature which can at once be subjected to test are exemplified by crossing back the F.1 impure tall plants with (*a*) the pure tall parents and (*b*) the dwarf plants—which are all pure. Using as before letters to denote the material factors at work, the pure breeding tall plants and dwarfs have the constitution TT, DD on the hypothesis outlined, since their character depends on factors inherited

from both parents : the impure plants F.1 have the constitution TD or DT. By crossing TD with TT we should get two types of offspring TT and TD, equal numbers of pure and impure tall plants. Also by crossing TD with DD, we get two types of offspring TD and DD, equal numbers of impure tall and pure dwarf. Mendel tested and verified these and other implications ; and all subsequent inquiry has confirmed the anticipations raised.

He was thus led to regard inherited characters as dependent upon unit factors derived from both parents, maintaining their separate entities throughout the entire life-cycle, and finally separating in the formation of the gametes, so that with respect to any single pair of factors one-half of the gametes contain the factor derived from one parent and the other half contain the factor contributed by the alternate parent. This is Mendel's first law of genetic segregation. For the sake of convenience we may here introduce some necessary technical terms. An individual which receives, like the " impure " F.1 tall plants, dissimilar factors from his parents is said to be *heterozygous* in contradistinction to the *homozygous* (dwarfs and pure tall) type. The character which appears to predominate, if its material forerunner is present in the fertilised egg, is said to be *dominant* in contradistinction to the *recessive* character, which is only manifest when both the gametes contribute its material forerunner.

Dominance is not a universal phenomenon. For instance, if we cross individuals from pure stocks of the red and white varieties of the flowering plant popularly known as *four o'clock* or botanically as *Mirabilis jalapa*, the F.1 generation bear only pink flowers. If these F.1 heterozygotes are selfed or crossed *inter se*, the F.2 generation is composed of reds, pinks, and whites, in the proportion 1 : 2 : 1. This would correspond to the 3 : 1 ratio if the heterozygotes were similar to one or the other type of

homozygote. In the case of the Andalusian fowl, already quoted, the F.1 individual produced by crossing black and splashed white birds is blue. Consequently the mating of Blue Andalusian fowls results in producing black and white offspring. Hence, if we wish to obtain blue individuals it is more profitable to mate blacks with whites, giving a heterozygous generation of blues only. The effect of crossing the blue heterozygotes among themselves is to raise a progeny of blacks, blues and whites in the ratio of 1 : 2 : 1. In these examples the heterozygote is intermediate between the parental homozygous types. In the inheritance of the white colour of Leghorn fowls, we encounter an instance of what may be called incomplete dominance ; for, if mated with an individual of a coloured strain, the heterozygous individuals are white with a few coloured tail feathers. Statistical analysis in fact shows that dominance is never absolutely complete. Whatever be the degree of resemblance between the F.1 generation of a cross between pure stocks and the parental types, the factors remain distinct and recombine to produce pure parental types again in the F.2 generation.

Of the physical nature of dominance we know little. An analogy will help the student to appreciate the question of dominance in its true perspective. Sodium and potassium yield colourless salts with most common acids, but the permanganates of both are purple in solution. The salts of copper are generally of a bluish or greenish tint in solution. In the one case the anion, in the other case the kation is the dominant factor in determining the physical property of colour. In neither case does the other component behave in any reaction with less characteristic efficacy on account of its presence being seemingly masked. So in the process of hereditary transmission the recessive factor is just as important as the dominant factor ; it is only in its bodily expression that the two are differentiated.

Though Mendel spoke of unit factors, it must not be imagined that a definite character distinguishing two related forms need only depend on one factor difference. Mendel was particularly fortunate in hitting upon a form in which there exist a number of strains which differ with respect to single pairs of unit factors. Had he studied, for example, the inheritance of the " walnut " type of comb which occurs in the Malay breeds of domestic fowl, he would have had a more difficult problem. The " rose " comb of Wyandottes and the " pea " comb of the Indian Game breeds are each dominant to the single comb of the Leghorn, Sussex and Rhode Island breeds. The " walnut " comb can be produced by crossing individuals with the Rose and Pea types of comb. A pure individual with a walnut comb crossed with an individual from a single comb breed would give an F.2 with walnut, rose, pea, and single combs all represented, because the walnut type differs from the single comb in respect of two pairs of factors, namely, those responsible when present alone for the pea and rose types. In the crosses which have been previously discussed, character differences in which only one pair of factors are involved have been deliberately selected for the sake of simplicity. In studying inheritance the geneticist often meets with apparently well-defined characters distinguishing two races of animals or plants which present a multiplicity of factorial differences, but it has been shown increasingly that apparent exceptions to the law of genetic segregation fall into line when the data are fully analysed.

The important point which emerges is that the original parental types in a cross between pure-bred parents reappear in their original purity, and in definite numerical proportions. To emphasise the latter a table of some of Mendel's crosses is given on the next page:

MENDEL'S DATA

Structure.	*Property*	*Dominant.*	*Recessive*	*Ratio in F.2*
Seed ...	Form	5,474 round	1,850 wrinkled	2.96 : 1
Reserve material in Cotyledons	Colour	6,022 yellow	2,001 grey	3.01 : 1
Seed-Coats ...	Form	822 inflated	299 wrinkled	2.95 : 1
Seed-Coats ...	Colour	705 grey	224 white	3.15 : 1
Unripe pods	Colour	428 green	152 yellow	2.82 : 1
Flowers ...	Position	651 axial	207 terminal	3.14 : 1
Stem ...	Length	787 tall	277 dwarf	2.84 : 1
		14,949	5,010	2.98 : 1 or 3 : 1

Side by side with this the reader may compare the following table showing the consistency of Mendel's observations in one of these crosses with those of later investigators:

Investigator	*Yellow Per cent.*	*Green Per cent.*	*Total*
	No. %	No. %	
Mendel, 1865	6,022 (75.05)	2,001 (24.95)	8,023
Correns, 1900	1,394 (75.47)	453 (24.53)	1,847
Tschermak, 1900 ...	3,580 (75.05)	1,190 (24.95)	4,770
Hurst, 1904	1,310 (74.64)	445 (25.36)	1,755
Bateson, 1905	11,902 (75.30)	3,903 (24.70)	15,806
Lock, 1905	1,438 (73.67)	514 (26.33)	1,952
Darbishire, 1909 ...	109,090 (75.09)	36,186 (24.91)	145,246
Totals	134,707 (75.09)	44,692 (24.91)	179,399

It must be remembered that the predictions of the law of segregation are statistical predictions. They depend ultimately on the experience known as the Law of the Constancy of Great Numbers, and our conclusions must bear the scrutiny of the mathematical requirements of the theory of

error which is founded on that law. To take the simple case of a 3 : 1 ratio, the assumption made is that, since two kinds of egg or sperm are formed by a heterozygous individual, there should be an equal chance of any egg being fertilised by either of two sorts of sperm (that carrying the maternal and that carrying the paternal factor). Similarly it is assumed that there is an equal chance that any sperm will fertilise one or the other type of egg. On this assumption the 3 : 1 ratio follows, if one of the parental characters is dominant. But since the assumption itself involves the idea of *chance* the conclusion is subject to the laws of chance. Obviously we cannot get a three-one ratio from a litter of three kittens. In experiments on inheritance in a common South African species of bean weevil, Dr. Skaife crossed the dominant black form with a red recessive mutant, and obtained in the second crossbred generation 347 black and 119 red individuals. For this number of individuals the 3 : 1 ratio requires two classes differing from 349.5 and 116.5 by a probable error of approximately 6. That is to say, it is as likely as not that the actual figures will exceed or fall short of these numbers by 6. The observed figures differed by much less than the probable error. An exposition of the methods used in determining the probable error of Mendelian ratios lies outside the scope of this book.

Mendel's investigations included an enquiry into what happens when two different pairs of characters, each depending on a separate pair of factors, are involved in a cross between pure-bred parents. The actual results of a cross between a strain of peas with green wrinkled seeds and yellow round seeds, or of peas with green round and yellow wrinkled seed respectively will be understood by referring to Fig. 72. The ratios of the double dominant, the two classes of single dominants and double recessives which Mendel obtained in all his crosses was 9 : 3 : 3 : 1, as should occur if the yellow-green factors and the round-wrinkled factors

behave quite independently of one another. Mendel formulated this result as a generalisation sometimes known as Mendel's Second Law. It is not, however, a law in the same sense as Mendel's First Law, of *segregation*, which we have deduced above, for it is only applicable to certain cases, and as we shall see later, the exceptions are of more theoretical interest than the rule. Here again an analogy from chemistry will help. The fundamental law of chemical combination is the law of constant proportions. The law of multiple proportions is no more than a statement of certain experiences that the pioneers of chemistry encountered in dealing with some of the compounds that were first investigated. Had they started with the hydrocarbons, they would have encountered no such simple relations. Both the law of multiple proportions and the second law of Mendel are historically important, because they aided the enunciation of hypotheses, which once stated were broad enough to take in other possibilities. We shall leave a consideration of the 9 : 3 : 3 : 1 ratio of Mendel's original experiments till a later stage, approaching the problem henceforth in a somewhat different manner.

The Chromosome Hypothesis. Mendel spoke of *factors* which determine the characters which organisms display under appropriate environmental influences. But all that is meant by heredity must refer to the contributions which the sperm and the egg make to the new individual. Can we go further, and identify within the sperm or egg the material entities which travel along the "germ track" through innumerable cell divisions, and finally separate in the formation of the gametes? Can we detect the existence of anything which behaves as our "factors" have been seen to behave?

Mendel's method leads to the conception of material units present in the fertilised egg in duplicate, and segregating before the formation of the gametes into maternal

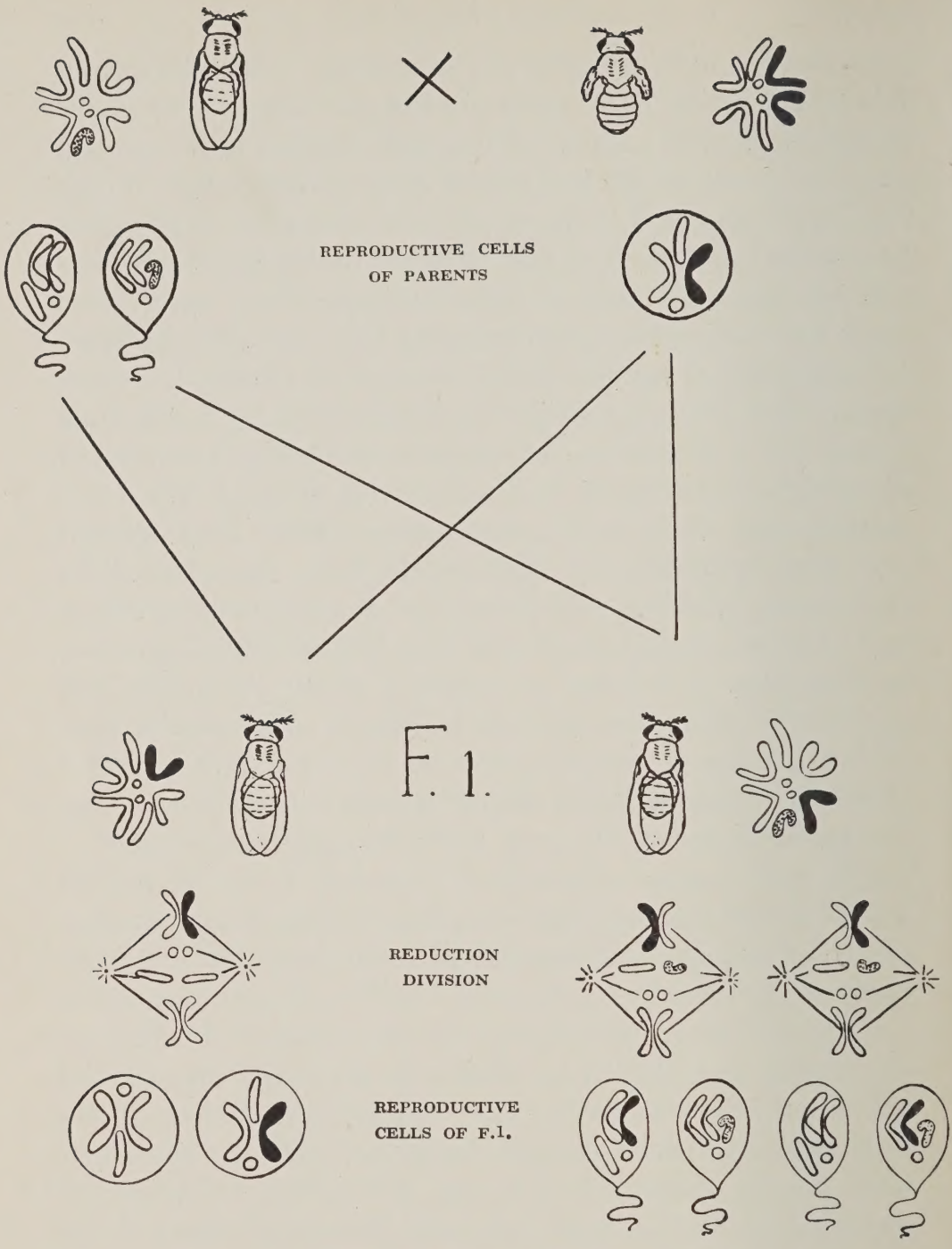

FIG. 69—DIAGRAMMATIC REPRESENTATION OF THE FIRST GENERATION OF A CROSS BETWEEN THE WILD TYPE OF THE BANANA FLY AND THE VESTIGIAL-WINGED MUTANT

The cross involves a difference in one pair of chromosomes only, and the Y chromosome is stippled. Vestigial wing behaves like purple eye (p. 149).

and paternal components, one member of each pair and one

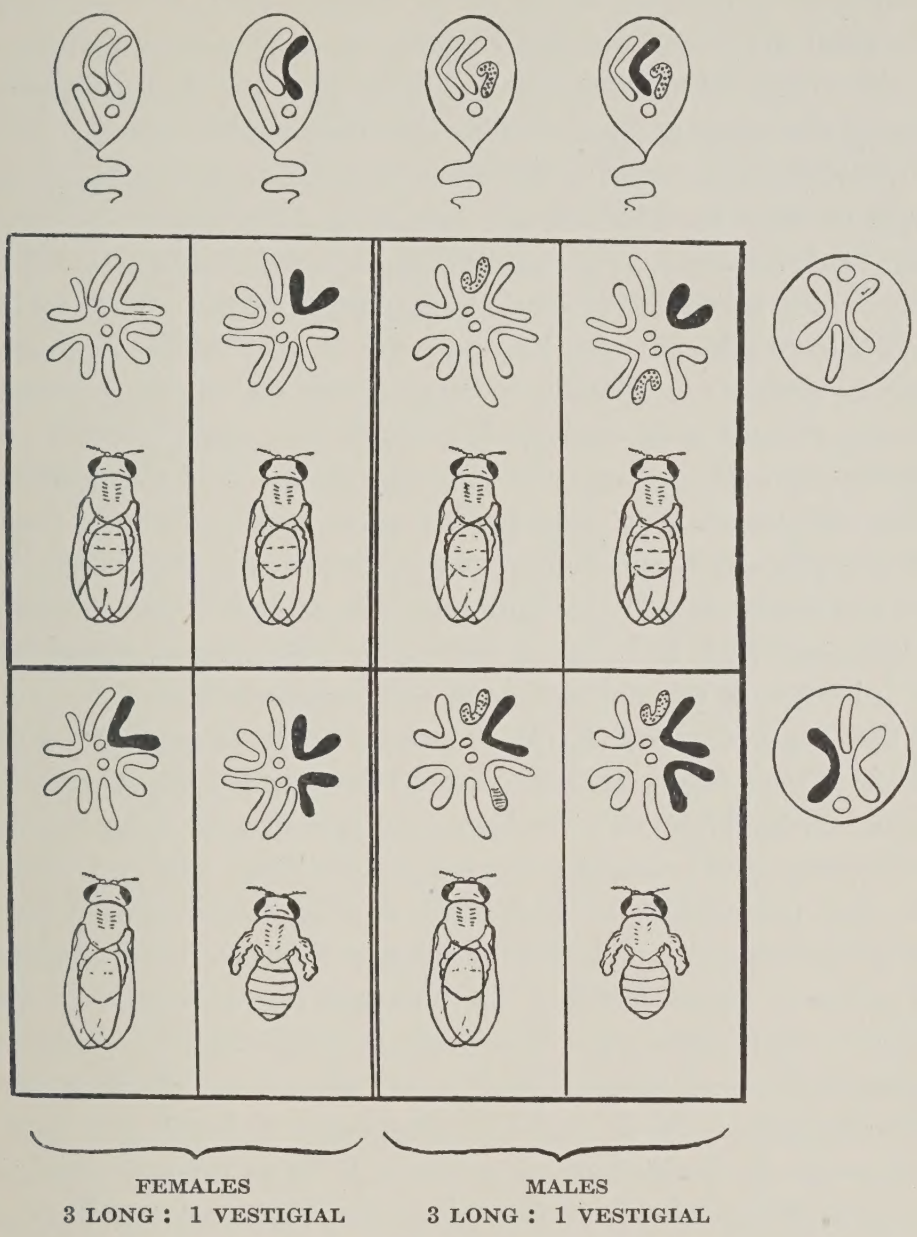

FIG. 70—CONTINUATION OF FIG. 69

Showing the numerical consequence of mating the first cross-bred generation of flies *inter se*.

only being present in each gamete. As is now known, the chromosomes in all animals and plants are present in the

fertilised egg in twice the number found to be present in the gametes. Furthermore, in many animals (and plants) from the most diverse phyla, the chromosome complex of a species is characterised not only by a definite number, but a definite configuration. It is possible to distinguish among the chromosomes pairs of different sizes and shapes (this is true both of man and the frog), and the maintenance of this constant configuration implies that when reduction takes place one member of each pair passes into each gamete. In other words, the chromosomes are present in the fertilised egg in pairs, segregating in the formation of the gametes into paternal and maternal components, one member of each pair and one only being represented in each gamete. The identification of the chromosomes as the material basis of the phenomenon of segregation immensely simplifies the deeper study of genetical phenomena, and the most striking advances which have been made of recent years in the study of inheritance are the outcome of this correspondence.

The application of Mendel's principles to animals was first made by Bateson and Cuenot independently in 1902, the year in which Sutton's work shewed the analogy between the behaviour of chromosomes and the material entities which Mendel postulated as the basis of biparental inheritance. In 1912 Morgan and his co-workers at Columbia commenced a series of investigations on *Drosophila melanogaster*, the fruit fly or banana fly. This little creature has almost every conceivable advantage for the purposes of genetical investigation. It is prolific. It passes through its entire life cycle in little over a week. It is eminently viable. It is easily cultured, requiring no food but rotting banana skins. It has only four pairs of chromosomes with marked individuality. With *Drosophila* one can do more in a year than could be achieved with cattle in several centuries. In Morgan's cultures about five hundred mutants or sports have appeared, and these mutants or sports, when mated

with their like, breed true to type. Thus the interrelation of the mutant characters in their mode of inheritance has been studied with a thoroughness that has no parallel in genetical investigation.

To illustrate the more concrete interpretation which the chromosome hypothesis affords, let us take a cross between one of the mutants of Drosophila and the pure wild type. The normal, *i.e.* wild type, banana fly has red eyes. There is a variety which has appeared as a sport distinguished by purple eyes. When a purple-eyed mutant is crossed to a wild type individual of pure stock all the F.1 generation are red-eyed. These red-eyed individuals, when mated among themselves, give offspring of which one quarter are purple-eyed and three quarters are red-eyed. If instead of crossing the F.1 individuals with one another we mate them with purple-eyed mutants, half of their offspring are purple-eyed and half are red-eyed. Now let us suppose that the purple-eyed form arose because a sudden change took place in one pair of chromosomes. The individuals of the first generation of our original cross will receive a chromosome of this pair from the purple-eyed parent and a chromosome of the same pair from the wild type parent. So the first generation will consist of individuals which possess one pair of chromosomes the two constituents of which are not the same, *i.e.* a pair of which one member has undergone the change referred to and one member has not. From the result it is evident that an individual will not be purple-eyed unless both members of this particular pair have undergone the change called a *gene*. When reduction occurs in the germ cells of the crossbred flies there will go to one pole a member of this pair carrying the purple-eye gene and to the other pole a chromosome of the same pair unmodified. So in the case of the male F.1 this pair of chromosomes will be represented in one half of the ripe sperm by a member that has the mutant gene and in the other half by a member that has

not. Similarly with the eggs produced by F.1 females. Thus a sperm which possesses the mutant chromosome will as often, on the whole, fertilise an egg which has it or an egg which has not. But for every sperm which has the mutant chromosome there will be one in which this particular pair is represented by a chromosome unmodified. Sperms of the latter type again will as often as not fertilise an egg which has the mutant chromosome. Thus for every fertilised egg which has this pair of chromosomes represented by members both of which carry the purple-eyed gene, there will be one in which the pair in question is represented by members both of which are unmodified, and two in which one member is unmodified and the other carries the purple-eyed gene. This gives the proportion of one quarter purple-eyed individuals in the F.2. The student can deduce for himself with the aid of the accompanying diagrams the consequences of other types of cross (*cf.* Fig. 70).

Let us now consider a cross in which two mutant characters are involved. Wild banana flies are grey in colour and the wings extend beyond the tip of the abdomen. Sports have appeared that are distinguished respectively by dark body colour and vestigial condition of the wings. There are, as a matter of fact, several mutants of Drosophila which have a dark body colour; the one we shall deal with here is denoted by the term *Ebony*. When either of these sports are crossed to pure wild type flies, the first crossbred generation are wild type, and these mated *inter se* yield progeny one quarter of which are of the mutant type. Now when the ebony mutant is crossed to the vestigial-winged type (for brevity, "vestigial") the flies of the first generation are all wild type, and when bred *inter se* have progeny of which, if sufficiently large numbers are taken, one-sixteenth show both mutant characters, three-sixteenths are ebony, three-sixteenths are vestigial, and nine-sixteenths wild type. This numerical result will be seen to follow by the laws of

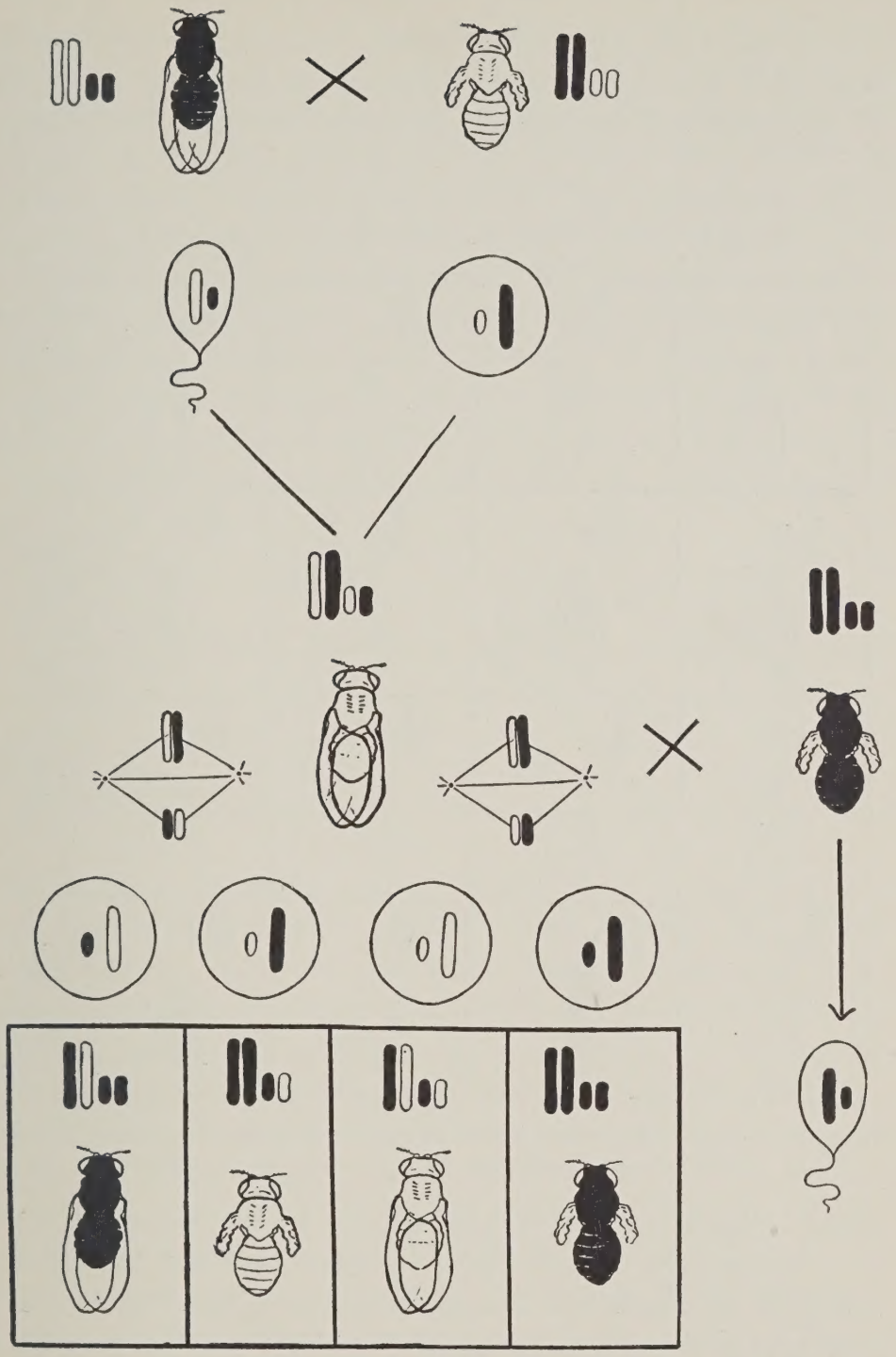

FIG. 71—CROSS BETWEEN THE "EBONY" AND "VESTIGIAL" MUTANTS OF THE BANANA FLY

The F.1 flies are crossed back to the double recessive type.

chance from the simple assumption that the change which originated the ebony condition occurred on a different pair of chromosomes from that on which occurred the change

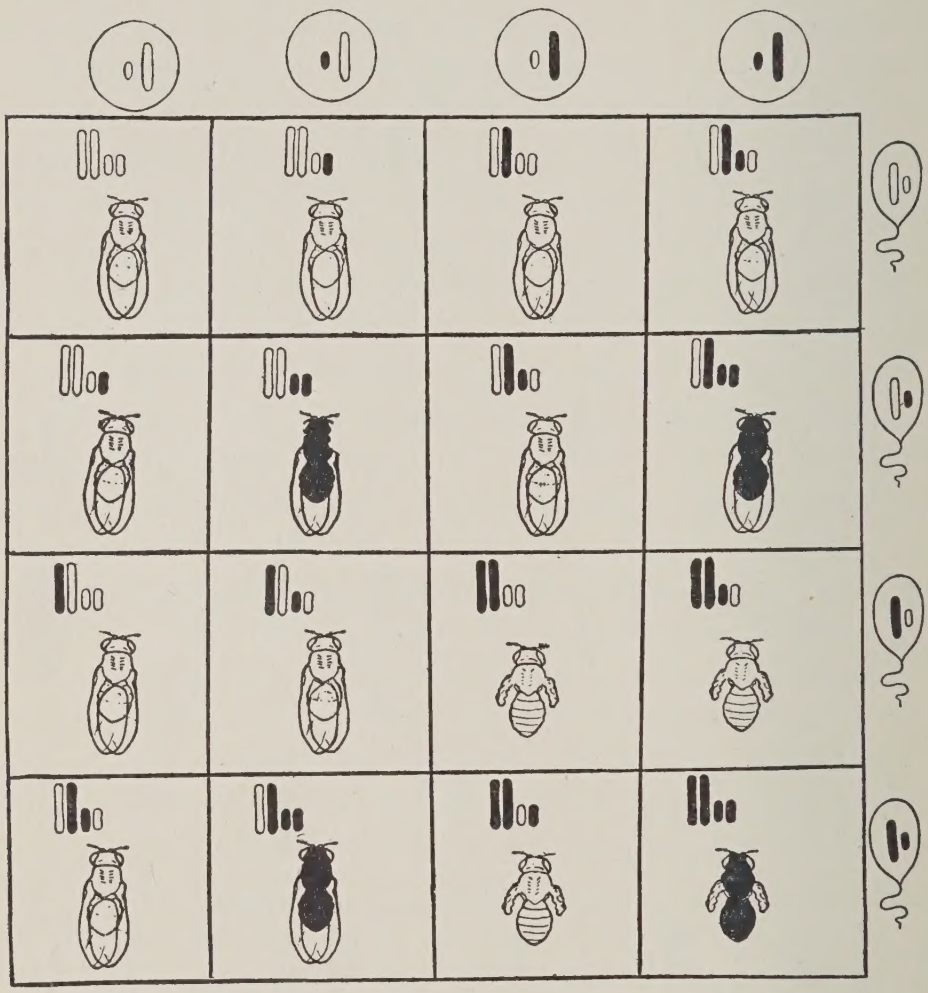

FIG. 72—RESULT OF MATING FIRST HYBRID GENERATION OF THE EBONY-VESTIGIAL CROSS OF FIG. 71 *inter se* (cf. text)

which originated the vestigial type. In the reduction division of the germ cells of the F.1 generation there will be two different configurations according as the mutant members of each pair go to the same or opposite poles (Figs. 71, 72) and the numerical recombinations can be simply deduced by representing chessboard-wise the fact that for every one of the

four different types of eggs fertilised by one of the four different types of sperm there will be a corresponding quartette fertilised by each of the remaining three types of sperm. If the F.1 flies of such a cross are bred with flies showing both mutant characters the four possible combinations will appear in the progeny in equal proportions.

We may here pause to interpret the inheritance of comb in fowls, a problem to which we have already referred. There are in poultry a large number of types of comb, of which the inheritance of four have been studied in relation to one another (Fig. 73). These are the rose comb of the Hamburghs and Wyandottes, the pea comb of

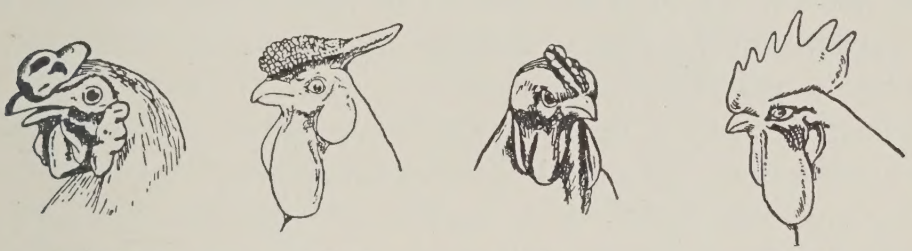

FIG. 73—FOUR DIFFERENT TYPES OF COMB IN THE DOMESTIC FOWL

the Cochins, the walnut of the Malays and the single comb of the Leghorns and other Mediterranean breeds. The difference between pea and single or between rose and single affects one pair of chromosomes only. That is to say, rose by single gives an F.1 all rose and an F.2 of rose and single in the ratio of 3 : 1. Similarly with pea and single, pea being dominant. If pure-bred walnut-combed fowls are crossed with singles the F.1 are all walnut type, the F.2 are walnut, rose, pea and single in the proportions 9 : 3 : 3 : 1. The same result follows a cross between pure rose and pure pea. The single-combed condition may be taken as the wild type, and the walnut type has arisen by mutant changes affecting two pairs of chromosomes, the change on one pair only producing the pea condition, and the change on the other

pair alone producing the rose condition. Here, it is to be noted, the mutant changes are both dominant, *i.e.* the mutant character is exhibited if only a single member of the modified pair of chromosomes involved is present. The student may illustrate this result diagrammatically with the aid of the chromosome symbolism as an exercise (*cf.* Figs. 71, 72).

We have thus arrived at the conclusion that the phenomena Mendel first investigated receive a simple explanation on the assumption that the chromosomes are the seat of those changes which lead to the appearance of individuals with new hereditable properties. We shall now proceed to show: (1) that the change or gene responsible for the appearance of a new hereditable property can be identified with a particular chromosome; and (2) that it can be identified with a definite position or locus on a particular chromosome. In everything about which we have concerned ourselves so far it is a matter of complete indifference whether the character with which we are dealing is introduced from the maternal or paternal side. But we know that there is one pair of chromosomes which is frequently unequally mated in one sex, so that any change which originated on this pair would not be symmetrically distributed as regards sex. In Drosophila the female has one pair of chromosomes (the first pair or XX) represented in the male by one element (X) of similar dimensions and another (Y) of different shape. Thus only half the sperms will carry an X chromosome. Now there is a large class—more than a hundred—of mutants of Drosophila which yield different results in crosses according as the mutant character is introduced from the maternal or paternal side. As an example we will select the type with white instead of red eyes. White-eyed males crossed to pure-bred red-eyed females produce offspring all of which are wild type. When mated *inter se* one quarter of their progeny are white-eyed

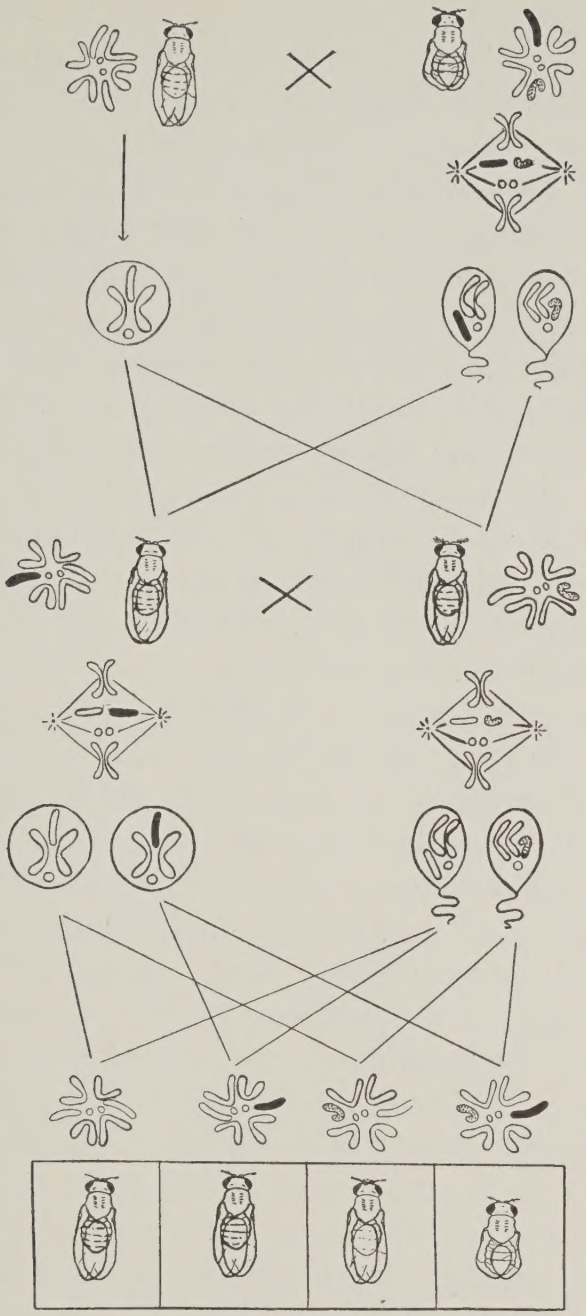

FIG. 74—A SEX-LINKED CROSS

The male of the mutant stock with *miniature* wings mated with wild type female, gives an F.1 all wild type; in the F.2 only the males are *miniature*. Compare the inheritance of white eyes discussed on p. 154.

but all these white-eyed flies are males. When white-eyed females are crossed to pure stock wild type males, only the female offspring of the first crossbred generation are red-eyed : the males are white-eyed, and the cross-bred flies mated *inter se* give offspring of which one quarter are white-eyed males, one quarter white-eyed females, one quarter red-eyed males and one quarter red-eyed females. To interpret this result we have to assume that the mutant condition arises on the X chromosome, and that it can override the effect of all the other chromosomes but not the influence of all the other chromosomes reinforced by another X chromosome from wild stock. In other words if a mutant X chromosome is present in the male the mutant condition will be exhibited, but the mutant condition will not be exhibited in the female unless both members of the first pair carry the mutant gene.

The phenomenon of " sex-linked inheritance," as this asymmetrical type of transmission is sometimes called, was first discovered by Doncaster (1906) in moths. In Lepidoptera the male is the XX type and the female XY or X. In the currant or magpie moth Abraxas, there is a pale-winged (lacticolor) mutant in contradistinction to the dark-winged (grossulariata) type. Doncaster set out to find why females of the lacticolor variety are much commoner than males. On breeding he found that dark-winged males crossed to pale females have all dark-winged offspring, which when mated *inter se* give dark-winged and pale moths in the ratio 3 : 1, all the pale moths being female. In the reciprocal cross only the males are of the dark type, and the F.2 are dark and pale males and females in equal proportions. Bearing in mind the difference between the chromosomes of moths and Drosophila the student will have no difficulty in following the interpretation of this result. An analogous type of sex-linked inheritance occurs in birds (canaries, poultry, etc.), as for instance in the dominant X-borne

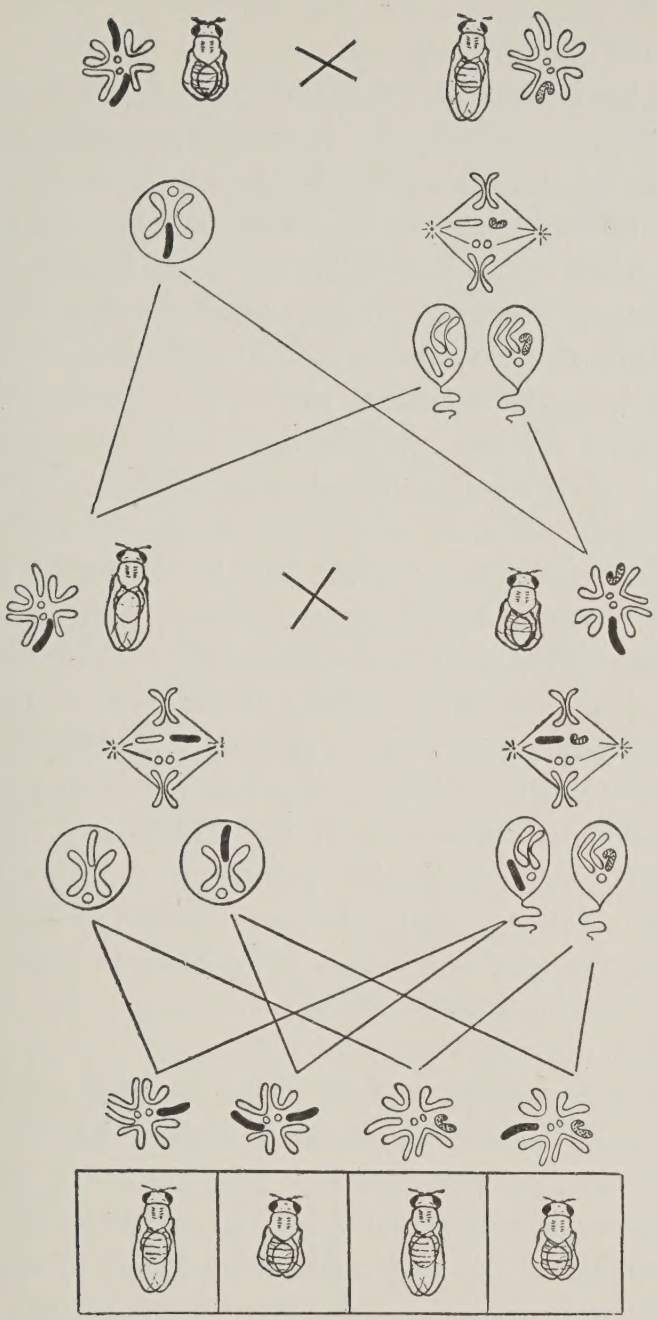

FIG. 75—RECIPROCAL CROSS OF FIG. 74

When pure wild males are crossed to *miniature* females the male offspring are *miniature* type.

mutant gene responsible for the barring of the plumage in the Plymouth Rock breed.

The coincidence between the genetic and microscopic data has been illustrated still further by the phenomenon of *non-disjunction*, described by Bridges in connection with several sex-linked mutant characters of which our original instance of white eye colour will serve as an example. There appeared among the white-eyed mutant stock of Drosophila certain strains of which the females, when crossed to normal red-eyed males, gave a certain proportion of red-eyed males and white-eyed females, in addition to the usual red-eyed females and white-eyed males alone. When the white-eyed female offspring of such abnormal matings were crossed back to red-eyed males they, in their turn, gave all four classes—red-eyed males and females, white-eyed males and females. The white-eyed females behaved like their mothers, giving abnormal results in all cases. Certain of the red-eyed females gave normal and others abnormal results in crossing. Of the male progeny the red-eyed individuals were normal, whereas only half the white-eyed individuals were normal, the remainder begetting daughters whose progeny was exceptional. Bridges found that in the abnormal white-eyed F.1 females the chromosome complex of the dividing body-cells was also abnormal—it showed a Y element in addition to the XX pair.

This is explicable on the assumption that at reduction of the eggs in certain exceptional cases the X elements failed to disjoin, so that the ripe egg contained either two X elements or none at all. If we represent the sperms of a red male as X′ or Y, two additional types of individuals will result from fertilisation by a Y or X′ sperm respectively, an XXY or white female, and X′O or red male. This accounts for the exceptional individuals in the F.1, and accords with the facts elicited. Next consider the results of back-crossing these XXY abnormal F.1 white females

to a normal X′Y male. According to whether the X elements segregate with respect to one another or the Y chromosome, the F.1 white females will have four types of eggs—XX, Y, XY, X. If these are fertilised by a Y sperm which does not influence red eye colour we get four types—(*a*) XXY white females, which will obviously behave in the same way, thus agreeing with breeding experience; (*b*) YY—individuals with this constitution cannot live; (*c*) XYY—white males which should produce XY sperms so that in crossing with normal white females daughters of the XXY type, producing exceptional progeny, would result; (*d*) XY—normal white males. When on the other hand, the same four classes of eggs are fertilised by an X′ sperm carrying the red factor, four red types of offspring would result, as follows: (*a*) X′XX—a triploid female, which usually dies; (*b*) X′Y—normal red males; (*c*) X′YX—red females with abnormal offspring; (*d*) X′X—normal red females. Thus, the non-disjunction of the X chromosome in the formation of the eggs of some of the females of the parental white-eyed stock accounts for the entire series of exceptional genetic phenomena which occur in these strains.

The Chromosome Map. Such evidence can leave very little doubt as to the legitimacy of envisaging the chromosomes as the material basis of the numerical relations which are found in breeding experiments, and the reader may refer to other works for abundant evidence pointing to the same conclusion derived from the study of inheritance in widely different types of animals and plants. We shall now go further and show that we can locate the changes which are responsible for particular mutant characters not merely on particular chromosomes but on a definite region of a particular chromosome, adhering for the present to that large group of mutant characters in the fruit fly whose behaviour corresponds to the distribution of the X chromosome.

The conclusion we have last stated is derived from a study of what happens in crosses which involve more than one sex-linked mutant character. There is a yellow-bodied mutant of the fruit fly which behaves, when crossed to wild stock, in a manner analogous to the white-eyed form. That is to say, the yellow females crossed to pure wild stock males give yellow males and grey females, and yellow males mated to pure wild type females give all grey offspring. If we cross a yellow female with white eyes and a pure stock wild type male, the female offspring are, as we should expect, wild type, but the males are yellow with white eyes (Fig. 76). When these are interbred an unexpected result occurs. A small but definite proportion of yellow individuals with red eyes and grey individuals with white eyes occurs. From this we must conclude that the same part of the chromosome is not involved in whatever is responsible for the yellow mutant on the one hand and the white eyed mutant on the other, for the two properties are separable. The numerical proportions in this case are approximately as follows :—

		%
FEMALES :	Wild type	24.725
	Yellow-white	24.725
	White-grey	.275
	Red-yellow	.275
MALES :	Wild type	24.725
	Yellow-white	24.725
	White-grey	.275
	Red-yellow	.275

Now suppose we make a cross involving these two mutant characters in a different way. Let us say we mate a yellow male and a white-eyed female. The first generation consists of white-eyed males and wild type females. These bred *inter se* give offspring of all four types :—

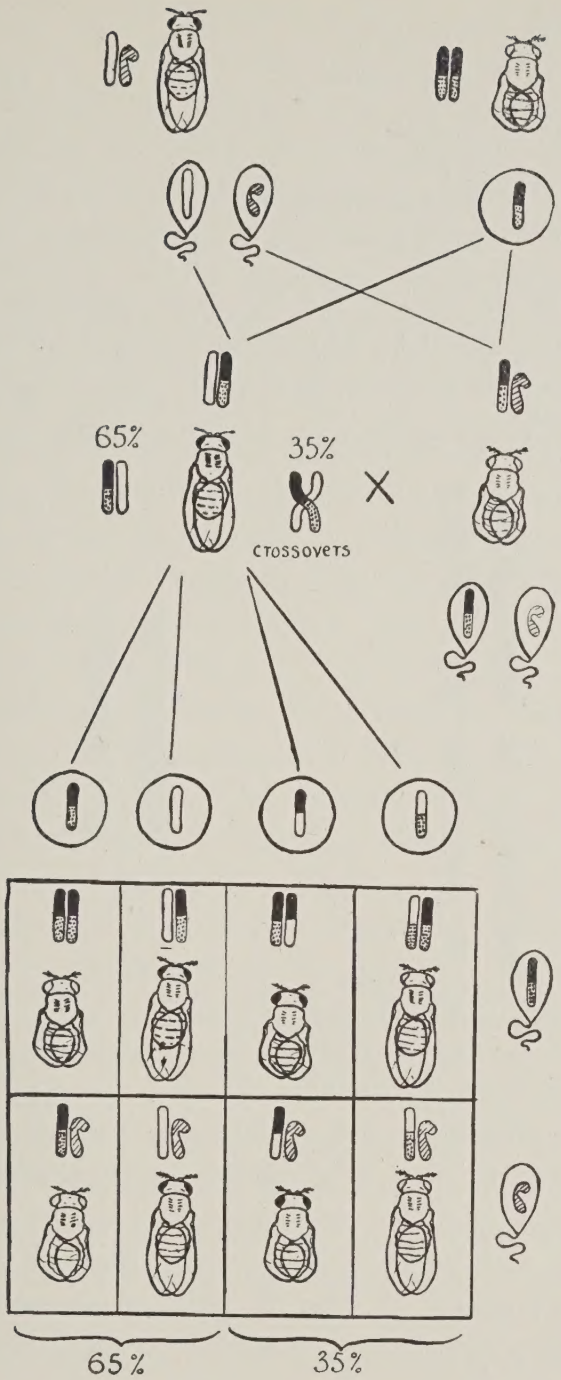

FIG. 76—CROSSING OVER BETWEEN TWO SEX-LINKED MUTANT GENES
The *white-eyed miniature* female is here mated with a wild type male.

		%
FEMALES :	Wild type	25
	White eyed	25
MALES :	Yellow	24.725
	White	24.725
	Yellow-white	.275
	Wild type	.275

Inspection of the figures for the males in these two crosses reveals that the extent to which the yellow and white mutant characters tend to become detached, when they are introduced from the same parent, is numerically equivalent to

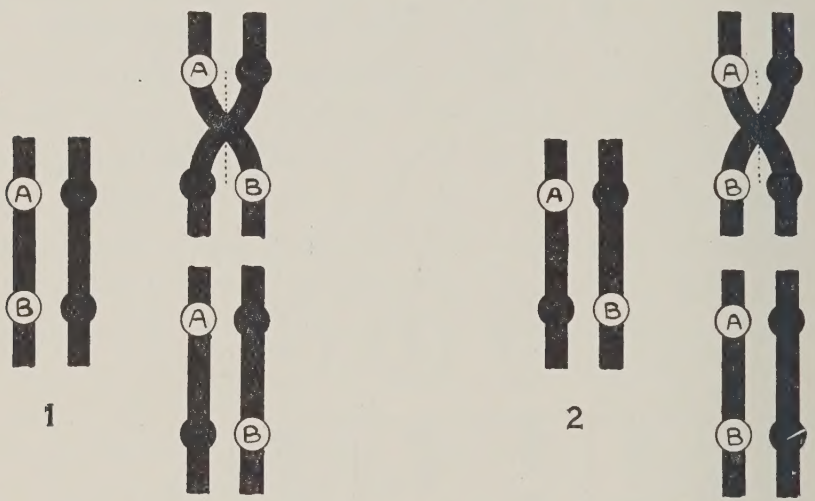

FIG. 77—DIAGRAM TO EXPLAIN CROSSING OVER BETWEEN TWO LOCI ON A CHROMOSOME—(1) IN THE CROSS BETWEEN YELLOW, WHITE-EYED FEMALE AND WILD-TYPE MALE ; (2) IN THE CROSS BETWEEN YELLOW MALE AND WHITE-EYED FEMALE

the extent to which they tend to come together, when they are introduced in the first place from different parents. This means that the two points or *loci* A and B, where the mutant genes are respectively located, become interchanged in the two members of the X pair of chromosomes in a definite proportion of cases (Fig. 77). It has been remarked by some microscopists that, in the process of pairing of homologous chromosomes in preparation for the reduction division, the attenuated filaments become twisted, and

since the split which occurs preparatory to the arrangement of the paired chromosomes on the spindle takes place longitudinally in the same plane as that in which they approximate, it has been surmised that a crossing over of corresponding lengths of homologous chromosomes occurs. It may also be added that in general the X and Y chromosomes of the XY individual remain distinct in the reduction phase. Now if this conclusion is correct certain consequences follow. On the assumption that the gene has a definite locus on the chromosome, we should expect that genes located in closely adjacent parts would tend to stick together more often than genes whose loci lie further apart.

This conclusion is capable of more numerical precision. If A B C are three points on the length of a chromosome, B being intermediate between A and C, then crossing over between the points A and C may take place in one of two ways. The length on which C is located may be displaced with reference to A carrying B with it, or the length on which C is located may be displaced with reference to A not carrying B with it. The first case involves the crossing over of the loci of A and B. The second involves transposition of the loci of B and C. Hence if the three points are located in the order stated the number of cases in which the loci of A and C are transposed will be the sum of the number of cases in which A and B cross over and B and C cross over. If the order of A B C is not given, the amount of crossing over between A and C may be the sum or difference of the cross over A—B and B—C (Fig. 80).

Let us see how this applies to the present case. Crossing over takes place between the locus of yellow and the locus of white in 1.1 per cent. of the reduction divisions in the formation of the eggs. There is another sex-linked mutant characterised by possession of wings which do not extend beyond the tip of the abdomen ; it is referred to as *miniature*. In a yellow miniature cross, the cross-over percentage

(cross-over value or C.O.V.) is found to be 34.3 and in the white miniature cross the C.O.V. is 33.2. The difference

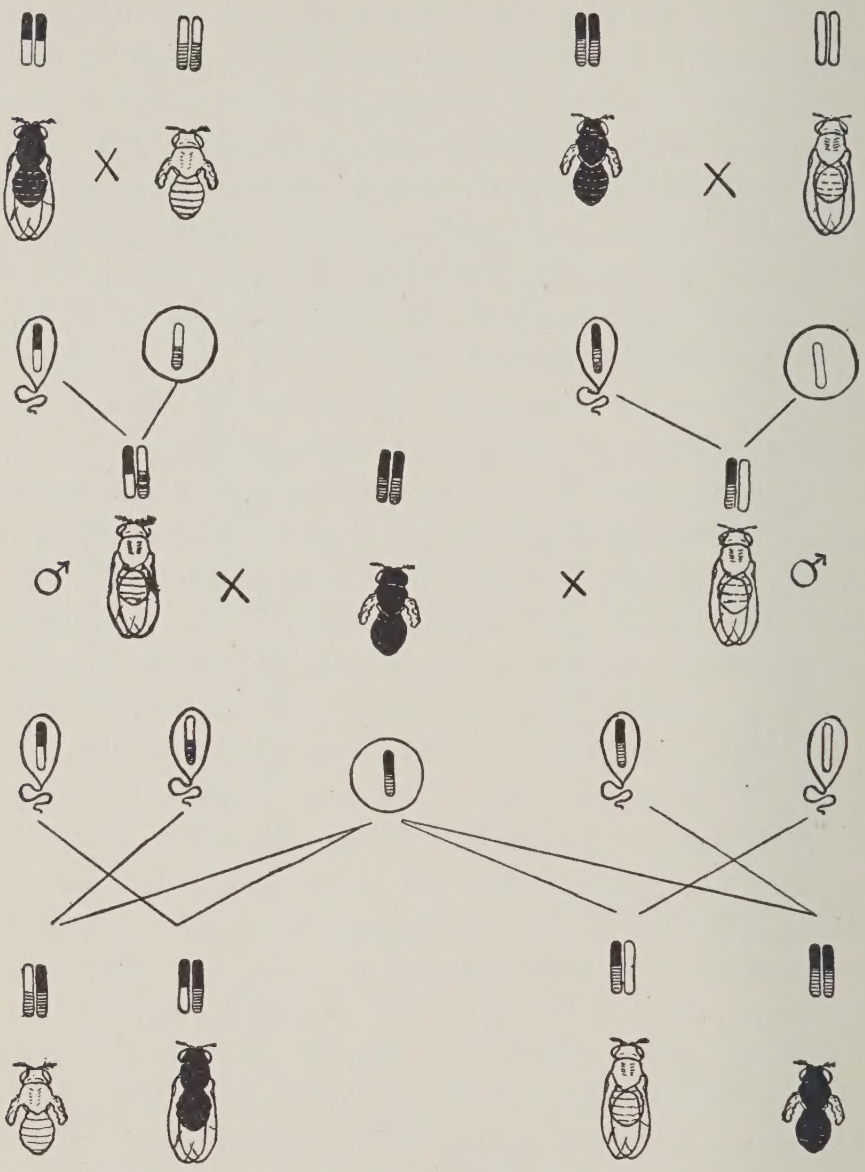

FIG. 78—LINKAGE IN A NON-SEX-LINKED CROSS

Effect of back-crossing to the double recessive female, the male offspring of a *black* × *vestigial* mating.

1.1 corresponds to the cross-over value for yellow and white. Thus the locus of white lies between the locus of yellow and miniature 1.1 units of length from the former and 33.2

units from the latter. This relation holds good for all the sex-linked mutant genes of Drosophila. Thus we can construct, as Morgan and his collaborators have done, a chromosome map.

Thus far we have confined our attention to one group of mutant characters which have their origin in changes which occur at definite loci on the X chromosome or first pair in Drosophila. Now Drosophila has four pairs of chromosomes all of which have been mapped out on the same principle. All that we have learned about the other chromosomes so far is that the genes for vestigial, ebony, and purple eye are not on the first (X) pair, and that ebony and vestigial are not on the same pair. There is in addition to ebony a dark coloured mutant which is referred to as black. When a " black " fly with vestigial wings is crossed back to the wild parent stock, the F.1 individuals are grey with long wings as in the ebony vestigial cross. Now, if the F.1 males are mated with females of the black vestigial type, the entire progeny are either grey with long wings or black with vestigial wings (1 : 1). A different result is obtained in the F.1 generation of a cross between a black mutant with normal long wings and a grey fly with vestigial wings. All the progeny are grey with long wings. But if these F.1 males are crossed back to the black vestigial females, the offspring are one half grey with vestigial wings. It is clear in this case (Fig. 78) that both results are capable of being interpreted as before, if we assume that a single pair of structural units is involved in the distribution of both recessive genes among the gametes. If now, instead of crossing back the F.1 males to the double recessive females, the reciprocal mating of the F.1 females to the double recessive male type is made, the result is slightly different. Taking first the case where both the recessive genes (black and vestigial) were brought in from the same parent, it is found that the back cross of the F.1 females instead of giving 50 per cent. black vestigial and 50 per cent.

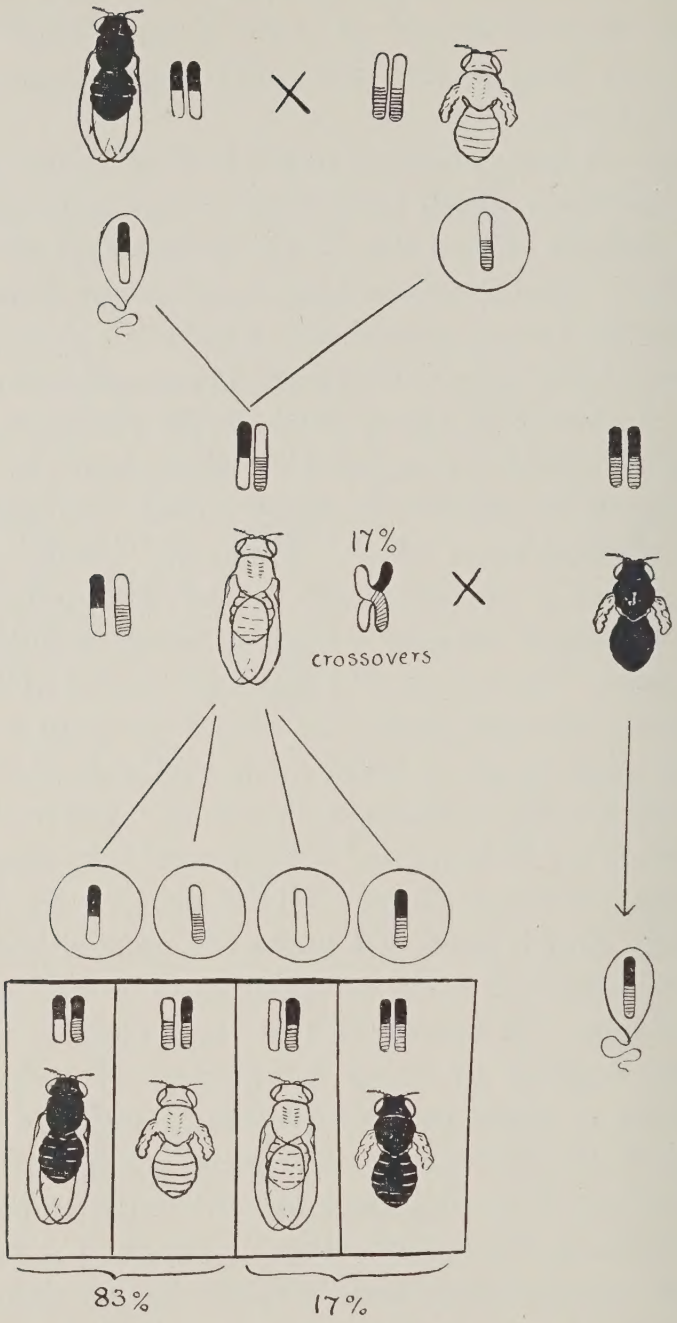

FIG. 79—CROSSING OVER IN THE BLACK-VESTIGIAL CROSS

Here the female F.1 of *black-vestigial* × wild type are crossed with the double recessive male.

grey long, produces 41.5 per cent. black vestigial and 41.5 per cent. grey long, together with 8.5 per cent. black long and 8.5 per cent. grey vestigial (Fig. 79). If the F.1 females of a cross in which only one recessive gene is introduced by each parent are back-crossed to the double recessive male, the progeny, instead of being 50 per cent. black long and 50 per cent. grey vestigial, are 41.5 per cent. black long and 41.5 per cent. grey vestigial, together with 8.5 per cent. black vestigial and 8.5 per cent. grey long. The numerical results are here amenable to interpretation on the assumption that there exists a single pair of structural units carrying both pairs of factors; but that in approximately 17 per cent. of the cases a crossing over occurs between the two components (Fig. 79).

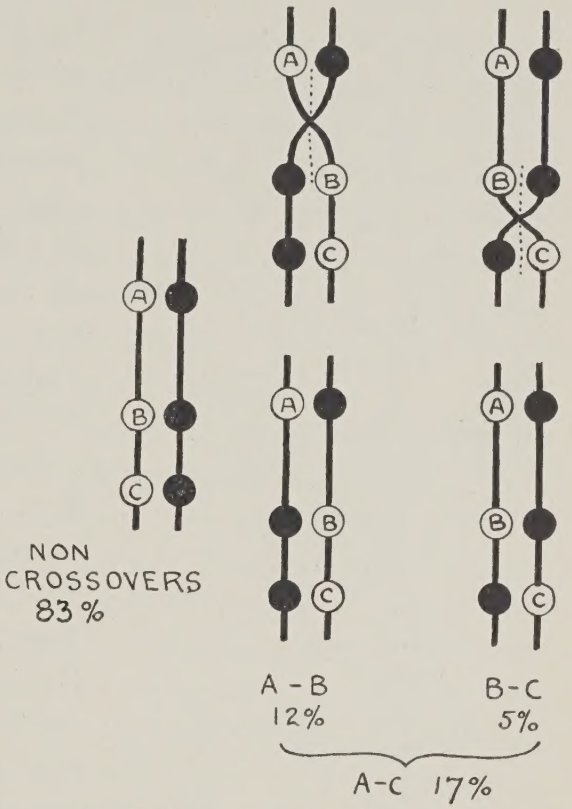

FIG. 80—DIAGRAM TO ILLUSTRATE THE LINEAR ARRANGEMENT OF THE GENES

The mutant with purple eyes is a simple recessive to the normal red-eyed condition. The mutant with the bent-up "curved wing" is a simple recessive to the normal long-winged condition. In a cross between individuals involving the vestigial and curved-wing characters the cross-over percentage was 8.2 based on a generation of 1,861 flies. The cross-over value for the purple and curved genes was 19.9,

based on a generation of 61,361 flies. The expected cross-over between vestigial and purple factors would therefore be 11.7. In an actual experiment in which 15,210 flies were reared, the cross-over value between purple and vestigial proved to be 11.8. The cross-over value for black and purple is 6.2, based on a generation of 51,957 flies. The expected cross-over value for the black vestigial cross would therefore be 6.2+11.8=18. In an actual experiment, based on 23,731 flies, the value 17.8 was obtained. To add yet another case in which the interrupted venation character, known as "plexus," was utilised, the cross-over value for the purple and plexus factors was 47.7, based on 350 flies. The expected value for plexus-black would thus be 47.7 — 6.2 or 41.5. In an actual experiment, involving 2,460 flies, the cross-over percentage was found to be 41.9.

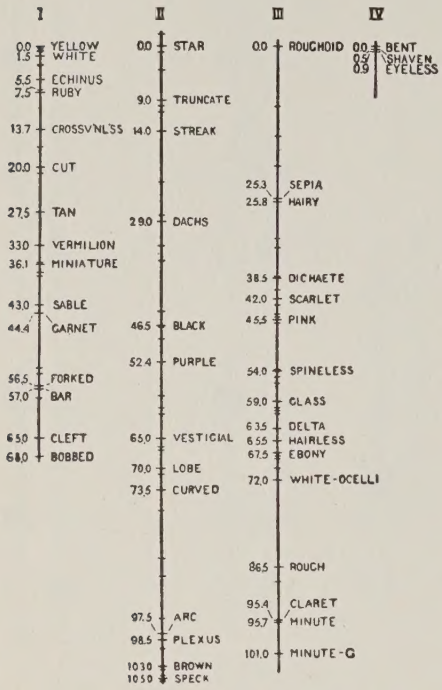

FIG. 81—MAP OF SOME OF THE MUTANT GENES OF DROSOPHILA

We thus see that there exists another group of characters in the fruit fly that can be arranged in a definite order on one of the remaining three pairs of chromosomes. The locus of purple lies between the loci of black and vestigial about twelve units of length from the latter and six from the former. All the mutant genes of Drosophila fall into four groups. Members of the same group tend to stick together —completely in the male with a definite amount of crossing over in the female. Members of different groups behave in a manner analogous to the ebony-vestigial cross. Thus

the number of *linkage* groups corresponds to the number of pairs of chromosomes and of these four groups one, the smallest, can be identified with the small "fourth" pair of chromosomes in Drosophila on account of abnormal genetical results obtained in crossing flies in which one member of this pair of chromosomes was found to be absent. Recently Punnett has shown the existence of seven linkage groups in the sweet pea which has seven pairs of chromosomes, and the arrangement of the genes in linear series has been shown to hold good for the sweet pea. We may conclude that the results obtained with experiments on the fruit fly are of general applicability.

The Universal Validity of the Principle of Segregation. We have now to turn to the consideration of a question of some importance in connection with the problems which we shall study in the second part of this book, namely whether the Principle of Segregation applies to all the hereditable properties of the organism. When Mendel's principles were first rescued from obscurity, few, if any, biologists would have been so bold as to assert the affirmative, and the majority were only willing to concede grudgingly a restricted validity to the Law of Segregation. Many stated explicitly that there were two sorts of inheritance, Mendelian and non-Mendelian. Every year since the beginning of the Mendelian Renaissance has witnessed some fresh success for the law of Segregation.

In answering the question we have just propounded, we may, therefore, pay due attention to some complications which puzzled the earlier investigators and gain some measure of confidence from their conquests. A great deal of confusion arose in the early stages through the use of the misleading term "unit character." A single clear cut anatomical difference may involve one or many genes. There is no relation between the magnitude of the one and the extent of the other. We have already considered the

inheritance of the walnut type of comb in the domestic fowl. The interpretation of such a case is directly deducible from Mendel's so-called second law. In a case involving changes on two pairs of chromosomes, neither of which displays dominance, instead of having only four types in the F.2 generation, we should have nine. The analysis of this result would not be at all obvious at first sight. If we had differences in three pairs of chromosomes determining a single character difference, the F.2 individuals would fall into one class with all three dominant characters, three classes with two dominant characters, three classes with one dominant character, and one class with no dominant characters in the ratio 27 : 9 : 9 : 9 : 3 : 3 : 3 : 1, if all three factor pairs showed dominance. But if neither member of any of the three pairs of characters showed dominance the number of classes would be twenty-seven instead of eight. In approaching the problem stated above, we must recognise, therefore, that extremely complicated cases may arise, when only a few factors are involved in the inheritance of some discrete anatomical or physiological difference distinguishing two strains. Thus, in a case where only four pairs of chromosomes come into play, no character being dominant to its alternative, the number of classes in the F.2 is 81. This alone should make any reflective person pause to think before quoting out of hand some difficult case that has not been analysed successfully as an argument against applying the principle of segregation consistently to the whole field of biparental inheritance. But even here, we have only exhausted a small fraction of the cases that at first sight present difficulty. Before we can gain the right perspective for a profitable discussion of this problem we must consider complications that arise from sources other than the mere number of genes involved. It is the successful analysis of such that justifies the confidence that modern workers feel in the general validity of their principles.

The first complication we shall consider is the "interaction" of genes. Two simple cases alone may be cited. On crossing a black and a red guinea pig, the F.1 individuals are of the mouse grey type known to breeders as agouti. The F.2 individuals are agoutis, blacks and reds in the ratio 9 : 3 : 4. This at once suggests that the red strain carries a dominant gene which modifies black, but does not modify red, so that the F.2 reds are composed of two classes, one which mated to black gives agouti and one which mated to black gives black. An example which specially bears on the species problem, is the case of two strains of sweet peas, both white and pure for white when inbred, but giving an F.1 of coloured individuals and an F.2 of 9 : 7 coloured to white when crossed. If strain A carries a gene absent in strain B, and strain B carries a gene absent in strain A, if both are located on different pairs of chromosomes, both having arisen in a coloured stock, both tending to make the colour white, and both recessive, the result necessarily follows from the fact that out of every sixteen three will have A in duplicate, three will have B in duplicate and one will have both A and B in duplicate, making seven whites.

An entirely different type of complication arises when there is involved in a cross a gene which affects the viability of the offspring. Such genes are classed together under the general term lethals. An immense number of cases of this kind have been thoroughly investigated with the most rigorous quantitative treatment. We shall only take a single example, that of a sex-linked lethal in Drosophila. Some females occur in Drosophila which have an excessive proportion of female offspring, in fact, a 2 : 1, instead of a 1 : 1 sex ratio. This result is explicable on the assumption that such females bear on one of their sex chromosomes a gene, which, if not compensated by a normal sex chromosome, prevents the individual surviving to maturity. As the male has only

one sex chromosome every male which inherits a lethal-bearing X chromosome from its mother dies. The hypothesis is tested rigorously by mating such females to white-eyed males, when the disturbances in the ratios of white-eyed and red-eyed individuals conform to the assumption that one maternal chromosome carries something which prevents the survival of her male offspring arising from eggs possessing it. In many cases of lethal genes infant mortality can be directly correlated with the disturbances of the normal ratio ; in others the condition may go back to a very early stage in development.

These considerations, however, do not exhaust all the possibilities which have to be taken into account. The most difficult, and for long the most insoluble, problem which the analysis of inheritance encountered was the transmission of characters which normally show a good deal of variability with reference to environment. In all the hereditable properties which we have so far considered the bodily expression of the gene has been clear-cut, and the environmental condition necessary to its appearance a normal concomitant of the conditions of life. When this is so, our problem is greatly simplified, and it is by the scrutiny of such simple cases that we gain knowledge which enables us to investigate the more intricate. Let us revert to the case of Mendel's experiments with tall and dwarf peas. The F.2 tall individuals are not all of the same size, nor are the dwarfs : each has a certain range of variability with respect to the local conditions in which the individual seed germinates. Nevertheless, they are distinct groups. Given proper conditions, the smallest tall is recognisably larger than the largest dwarf. In dealing with size characteristics, however, hereditary differences may not be so nicely defined. Often they can only be described in statistical terms. Two inbred stocks may differ by some average that is characteristic of the progeny of individuals

reared under identical conditions, but it may be quite impossible to distinguish the individuals themselves.

This makes ordinary experimental procedure impossible. But the problem is simplified, if the organism is hermaphrodite and self-fertilising, as are many plants. If we take beans from a mixed collection of the same species but not

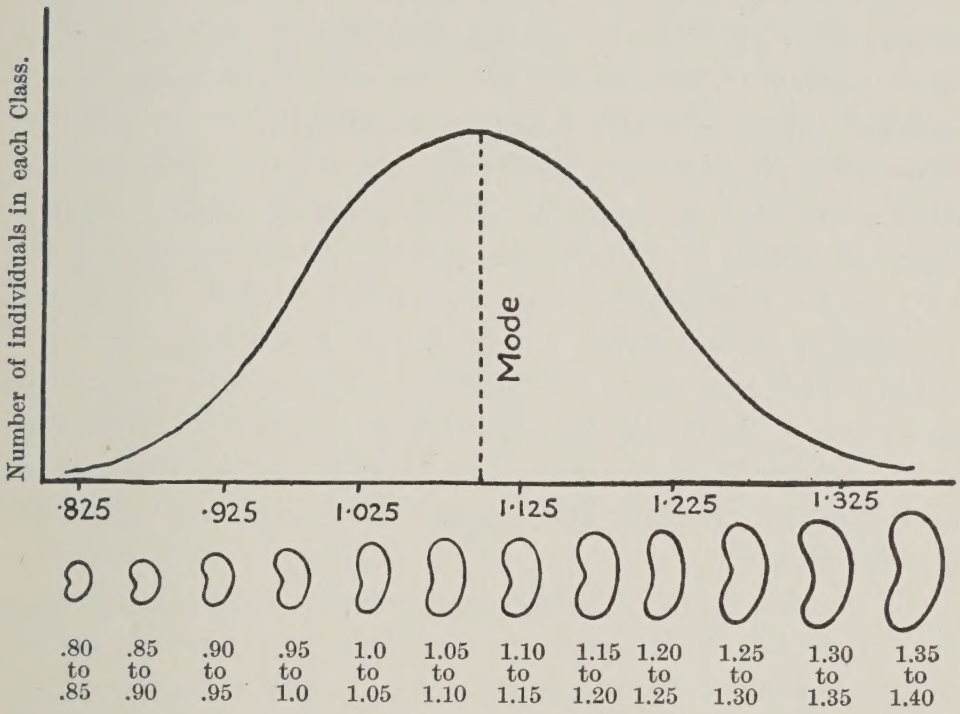

FIG. 82—NORMAL FREQUENCY CURVE ILLUSTRATED BY VARIABILITY IN WEIGHT OF BEANS

of the same parentage, and weigh them, we can arrange them in groups according as they fall within certain limits. On counting the number of beans in each group or class, we can plot a curve of which the ordinates represent the numbers in a class (class frequency) and the abscissæ correspond to the mean value of each class. In general the curve will have the shape indicated in Fig. 82. Now on taking individual beans, allowing them to germinate and seed by self-fertilisation, we find, as was first shown by Johannsen

(1909), that the frequency curves of many will be practically identical in form with those of the original mixed population. Others, however, will have curves whose most fashionable value or *mode* corresponds to a higher or lower class than that of the mixed population. If we take any of the offspring of a bean whose progeny show a high or low modal value, allow it in turn to germinate and seed, we find that the modal class of its grandchildren will be the same as that of their parent. Thus we can have two stocks of beans distinguished only by the fact that they regularly produce offspring whose frequency curves for the size character in question display a constant difference of the modal class value, yet when equal numbers of individuals of both stocks are mixed the two series might so completely overlap that the mixed population would yield a frequency curve with only one peak. The only way in which we can test our hypothesis is to see what would be expected to happen if Mendelian principles are applied to the case of highly variable characters, and observe whether our expectations coincide with the observed facts.

Unless sex-linked factors are involved in a cross between parents of two different pure-bred strains, all the individuals of the F.1 must be genetically alike. Any differences that exist among them *inter se* will be due to external agencies alone. The differences between individuals of the F.2 will always be the result, on the other hand, of both genetic differences and bodily variability, and there can never be more genetic types in any succeeding generation than appear in the F.2. Hence, if the principle of segregation applies to cases like height, weight, girth, growth-rate, etc., cases that is, where the character in question is a very variable one, any cross between individuals of pure strains differing with respect to the modal value of the character must always conform to a simple rule: maximum variability in the F.2 and minimum variability in the F.1. The

test is one which has been satisfactorily applied to many cases.

The mathematical treatment of this problem, when a large number of genes are involved, is complicated, but the simple case in which one factor difference is concerned can be set forth without recourse to elaborate statistical treatment. Let us take the case of two parents of stocks whose progeny give the curves P.1 and P.2, which are supposed to be based on the same number of individuals, let us say 1,000. The two series overlap but their modes are different. Let the modal value for the F.1 curve for the sake of simplicity

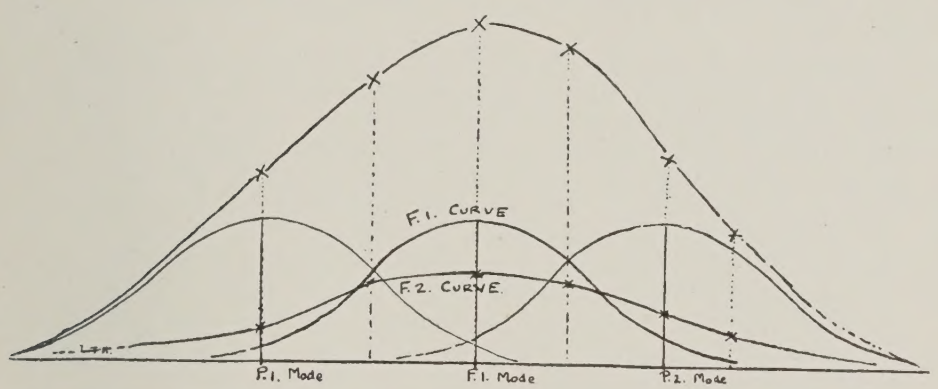

FIG. 83—CURVES TO ILLUSTRATE MAXIMUM VARIABILITY IN THE SECOND GENERATION (see text)

be taken as intermediate, and the F.1 curve in Fig. 83 be plotted for the same number of individuals as the P.1 and P.2. Now the F.2 generation will consist of three genetic types, the two parental types and the F.1 type, and for each individual of the parental types there will be two of the F.1 on the principle of segregation. Let us, therefore, add each ordinate of the parental curves to twice the value of the corresponding ordinates of the F.1. The new dotted curve will be based on 4,000 individuals. To reduce this to comparable dimensions with the P.1 and P.2 curves we must divide each ordinate by 4. This gives us the flat curve of the F.2. The flatness of this curve shows the greater

variability of the F.2, and affords a mathematical test of the validity of the Principle of Segregation as applied to highly variable characters. A few applications of this method of analysis to animals (number of tail feathers in pigeons, e.g.) have been made, and it has been extensively tested in plant breeding.

PART II

THE ORIGINS OF LIVING MATTER

But the mortallest enemy unto knowledge, and that which hath done the greatest execution upon truth, hath been a peremptory adhesion unto authority; and more especially, the establishing of our belief upon the dictates of antiquity. For (as every capacity may observe) most men, of ages present, so superstitiously do look upon ages past, that the authorities of the one exceed the reasons of the other. Whose persons indeed far removed from our times, their works, which seldom with us pass uncontrolled, either by contemporaries, or immediate successors, are now become out of the distance of envies; and, the father removed from present times, are conceived to approach the nearer unto truth itself. Now hereby methinks we manifestly delude ourselves, and widely walk out of the track of truth.—Sir Thomas Browne's *Pseudodoxia Epidemica.*

Chapter VIII

THE EVOLUTIONARY PROBLEM

SCIENCE deals, not with values, but with relations between objects in the external world. In the first part of this book we dealt with the relation between living and non-living matter, as exemplified by those kinds of living matter which are denoted by the term animals. Living beings, however, differ not only from inanimate objects but also from one another. Hence another object has engrossed the attention of those who study them, namely the relation between different forms of living matter. As we study the characteristic differences between living and non-living matter, we are faced with one fundamental question. Is the gap between living and non-living matter beyond all comprehension, or is it possible to formulate the same underlying principles of mechanism in the world of animate and inanimate nature? As we study the different kinds of living matter, or, in more customary language, different species, we shall find ourselves involved in another general problem. Is the gap between different species one that cannot be bridged by any ascertainable natural process, or can we interpret the diversity of animal life in terms of some natural process of which we have direct experience? Interest in this question is really older than the attempt to answer the more fundamental problem, and it has obsessed the biological world ever since the detailed study of differences between species began in the middle of the eighteenth century.

We have so far largely confined ourselves to three types of living matter, the frog, the banana fly, and Man. Each of these is customarily called an animal, and each displays certain characteristics which it shares with the others in contradistinction to all things which are not called animals, but each in addition has many peculiarities which distinguish it from the remaining two. From very early times, students of animals classified them according to the degree of resemblance that they display with regard to one another. Aristotle's History of Animals is an early example of this attempt to draw up such a classification. After the rise of Christianity there was little further progress in the detailed study of animals except in so far as the Moorish physicians kept aflame the torch of free enquiry. Until the eighteenth century the work of classification of living creatures was mainly confined to plants. In 1757 Linnæus systematised the existing state of knowledge in a monumental work, the *Systema Naturæ*, in which most of the conventions now employed in grouping animals and plants according to the degree of resemblance they display to one another were first laid down.

The Greeks had distinguished by name some five hundred plants in all. In the Arabic Universities of Bagdad, Toledo and Cordova, the study of plants had been encouraged for medicinal uses, and in all about two thousand official herbs were recognised in the Moorish pharmacopœia. A great deal of the information they gathered was probably lost. But in those early Italian medical schools which were founded in the twelfth and thirteenth centuries as outposts of Moorish culture by Spanish and Portuguese Jews, the Latin and Hebrew texts of the Arab writers provoked a keen interest in the study of plants, which bore fruit in the Herbals of the early sixteenth century. In the Herbals many plants appear with twofold Latin names, *e.g. Trifolium pratense* in Gerard's *Herball*, but at first there was very little

arrangement of the subject matter, and no systematic key. As the number of plants of alleged medicinal value increased some method of codification became a sheer necessity, and through Gesner (1516-1565) and Caesalpinus (1519–1603) to Ray (1628–1705), we see a succession of attempts to classify the vegetable kingdom in some cases no less ambitious than that of Linnæus, who first adopted the binomial nomenclature (vide infra) for all organisms, and extended the practice of denoting each classificatory division by an appropriate Latin name to animals as well as plants.

The Species Problem. The problem formulated above has come to be known historically as that of the Origin of Species. A great deal of confusion has arisen from the use of this phrase. In classifying organisms various terms are employed to denote groups based on structural similarity. Of these terms the chief are phyla, classes, orders, families, genera and species. All these groups with the exception of the last are purely arbitrary descriptive terms, representing the impression which those who have studied a group of animals have gained regarding their similarities and differences. On the whole these impressions coincide to a very large extent. In spite of all the differences that exist in various works on systematic zoology, most animals that we meet fall into assemblages which are recognised by every one who has studied the subject. Nevertheless there is no clear cut test which can be applied to classification as a whole. Linnæus, however, gave to the term species a special significance which is of a more objective character than that of the class or genus. He made the species a breeding unit. In other words animals or plants come within the same species, if they breed readily with one another and produce offspring which do the same. Without doubt a very large proportion of the forms included by systematic zoologists do come within

such well-defined groups. But of many, and indeed the majority of animals placed in single species, we have absolutely no knowledge of their capacity to interbreed efficiently with members of other recognised species. Preserved materials, sent from different parts of the world, are described in museums, more often than not by observers who have never examined the animal in its natural habitat in the fresh condition. On the basis of such differences and similarities as can be detected in specimens collected and described in this way, new species are made daily. Comparatively small anatomical differences may be associated with the species barrier in the Linnæan sense, while very striking ones may exist within the limits of a single Linnæan species. It is therefore a pity that writers do not specify more carefully, whether they are speaking of a biological or Linnæan species or of a systematic or museum species.

Linnæus also adopted the convention of grouping species into larger groups which are denoted genera, each genus being referred to by the first of the two specific names. Genera were grouped in large assemblages called families usually named after some representative or common genus included therein and terminating like the Patrician families of ancient Rome in the suffix *-idae*. Families were assembled in orders, orders in classes. Classes are now placed in still larger groups which were introduced after the time of Linnæus, and are referred to as phyla. To illustrate the meaning of these terms we may again take as our three types, the frog, Man and the banana fly.

The Conventions of Systematic Biology. The common frog belongs to the genus Rana, which includes many species; among the best-known are *Rana temporaria*, the common European grass frog; *Rana esculenta*, the European edible frog; *Rana catesbiana*, the North American bull-frog; and *Rana silvatica*, a smaller North

American species. Rana is grouped with several other genera in the family Ranidæ. The Ranidæ, along with the Bufonidæ, a family which includes the common toads, and certain other families, is included in the order Anura. The order Anura with another order, the Urodela, which includes among other forms the Mexican salamander (*Amblystoma tigrinum*) takes in most of the animals included within the class Amphibia. The Amphibia is one of the six great classes placed in the phylum Vertebrata, the others being Cyclostomes (lampreys and hagfishes), Pisces (fishes), Reptilia (snakes, lizards, crocodiles, tortoises), Aves (birds), and Mammals (vide infra). The Vertebrata is one of a number of large assemblages (phyla) of animals of which the chief others are usually called nowadays: Porifera (sponges), Cœlenterata (corals, jellyfish, sea anemones), Echinodermata (starfishes and sea urchins), Platyhelminthes (flat worms), Nemathelminthes (round worms), Annelida (segmented worms), Arthropoda (insects, spiders, crabs, centipedes, etc.), Mollusca (snails, squids, clams). Any of the above groups may be subdivided. For instance, the South American toad of the genus Pipa, which carries its eggs in pits on the back of the female, is sometimes separated from all other Anura along with Xenopus, the South African clawed toad, in a sub-order Aglossa, distinguished *inter alia* by the absence of a tongue and the presence of a single median internal opening of the eustachian tube. Again, some authors group the Amphibia with birds, reptiles and mammals in a sub-phylum Tetrapoda, which comprises all Vertebrates with five-fingered limbs. Many authors make the Vertebrata a sub-phylum of a larger group, the Chordata, erected to take in some less familiar forms, such as the sea squirts and other forms which while lacking the characteristic Vertebrate sense organs (eye, labyrinthine organ, olfactory organ) cranial nerves and circulatory

system, display certain peculiarities of organisation which distinguish Vertebrates from all other groups.

Let us now turn to man. All living men, of whatever colour, creed, or political belief, are biologically a single species ; they can interbreed successfully. All living men, then, are placed in the species denoted perhaps inappropriately, *Homo sapiens*. A separate species is usually recognised within the genus Homo, *H. neanderthalensis*, to describe the heavy-browed men of the Old Stone age, though we are not really conversant with their ability to interbreed with modern men. Along with Homo are placed two doubtful fossil genera, *Eoanthropus*, the Piltdown man, and *Pithecanthropus*, the Javanese Ape-man, in the family Homindæ. The latter, together with the Simiidæ (Anthropomorphidæ) or ground apes, the Hylobatidæ or Gibbons, Cercopithecidæ or Old World monkeys and baboons, Cebidæ, the New World monkeys, Hapalidæ, the marmosets, and Tarsiidæ (a lemur-like form), are all included in the order Primates. The Primates, Lemuroidea, Ungulata (hoofed mammals), Cetacea (whales), Chiroptera (bats), Rodentia, Carnivora, Marsupialia (kangaroos and opossums), Monotremata (duck-billed platypus) and some other orders constitute the class Mammalia of the phylum Vertebrata. Mammals differ from the class Amphibia, in which the frog is placed, in a large number of points which we have already noted. In the first place, they are externally covered with hair, and the female suckles her young. The heart is four-chambered, and there is a diaphragm which partitions off the bony thoracic cavity from the abdominal region. There is a chain of three small bones in the mammal between the drum and the innermost part of the ear.

The banana fly of Morgan's experiments is *Drosophila melanogaster* (*D. ampelophila*). A number of other species of the same genus are known. This genus is placed in a family Drosophilidæ. Along with the Muscidæ

or house flies, the Syrphidæ or hover flies, the Culicidæ or gnats, which all have a single pair of wings, the Drosophilidæ are placed in the order Diptera of the class Insecta or Hexapoda. All insects agree in having a single pair of feelers, three pairs of legs and a body distinctly divided into three regions (head, thorax and abdomen). But insects share certain features which are shown by no other animals except the classes Arachnida (spiders, ticks and scorpions), Crustacea (crabs, barnacles, shrimps), Myriapoda (millipedes and centipedes), in particular, jointed legs of which the muscles are wholly enclosed in the hard skeletal portion. On this account a large assemblage or phylum, the Arthropoda, is erected to take in insects, crabs, spiders and the like. We shall deal in detail with various features which distinguish the Vertebrate organisation from that of the Arthropod at a later stage.

The System of Linnæus. The system of Linnæus divided the animal kingdom into six classes, Mammalia, Aves, Amphibia, Pisces, Insecta and Vermes. The first, second, and fourth correspond closely with the modern groups of the same name. The Amphibia in Linnæus' sense includes in addition to the Amphibia of present-day zoologists, reptiles and a number of forms like the sturgeon and shark, rightly transferred by Cuvier to the fishes. Nevertheless on the whole Linnæus' classification shows very much more knowledge about Vertebrates, man's nearest allies, than about any other animals. This reflects the origin of biology in connection with medicine, and indeed most of Linnæus' zoological data are referable to Hippocrates and Aristotle. The classification of Linnæus is really in broad outline that tacitly implied in some passages of Aristotle's Natural History, from which it differs mainly in formal presentation and greater detail, as far as it incorporates the labours of Gesner and Ray. Linnæus' class "Insecta" corresponds to the phylum which we call the

Arthropoda. Linnæus divided his Insecta into seven orders, in one of which, the "Aptera," he placed along with true wingless insects, in the modern usage of the term, all other Arthropods, namely, Crustacea, Arachnida and Myriapoda. The names of the remaining orders of Linnæus' "Insecta" are retained in classifications of insects still in use (Coleoptera—beetles; Lepidoptera—butterflies; Diptera—houseflies and gnats; Hymenoptera—bees, ants, etc.). In the sixth class, Vermes, Linnæus placed all animals other than Vertebrates and Arthropods. The outstanding feature of his scheme —illustrative of its anthropocentric bias—is that four of his six major divisions are now classes of a single phylum, the Vertebrata. In subdividing these Linnæus adopted many groups, *e.g.* the orders Primates (man, apes and monkeys), and Cete, or as we now say Cetacea (whales), which have been retained to the present day.

The classification of Linnæus (from *Syst. Nat.*, 12th ed., 1766) is as follows—the complete list of Linnæan genera being here reproduced[1]:—

Class I. MAMMALIA

Order 1. *Primates*
Genera: *Homo, Simia, Lemur, Vespertilio.*

,, 2. *Bruta*
Genera: *Elephas, Trichecus, Bradypus, Myrmecophaga, Manis, Dasypus.*

,, 3. *Feræ*
Genera: *Phoca, Canis, Felis, Viverra, Mustela, Ursus, Didelphys, Talpa, Sorex, Erinaceus.*

,, 4. *Glires*
Genera: *Hystrix, Lepus, Castor, Mus, Sciurus, Noctilio.*

,, 5. *Pecora*
Genera: *Camelus, Moschus, Cervus, Capra, Ovis, Bos.*

[1] Not with a view to memorisation by the student, who will find no difficulty in identifying the names from Museum specimens.

Order 6. *Belluæ*

Genera: *Equus, Hippopotamus, Sus, Rhinoceros.*

„ 7. *Cete*

Genera: *Monodon, Balæna, Physeter, Delphinus.*

Class II. Aves

Order 1. *Accipitres*

Genera: *Vultur, Falco, Strix, Lanius.*

„ 2. *Picæ*

Genera: (*a*) *Trochilus, Certhia, Upupa, Buphaga, Sitta, Oriolus, Coracias, Gracula, Corvus, Paradisea;* (*b*) *Ramphastos, Trogon, Psittacus, Crotophaga, Picus, Yunx, Cuculus, Bucco;* (*c*) *Buceros, Alcedo, Merops, Todos.*

„ 3. *Anseres*

Genera: (*a*) *Anas, Mergus, Phœthon, Plotus;* (*b*) *Rhyncops, Diomedea, Alca, Procellaria, Pelecanus, Larus, Sterna, Colymbus.*

„ 4. *Grallæ*

Genera: (*a*) *Phœnicopterus, Platalea, Palamedea, Mycteria, Tantalus, Ardea, Recurvirostra, Scolopax, Tringa, Fulica, Parra, Rallus, Psophia, Cancroma;* (*b*) *Hematopus, Charadrius, Otis, Struthio.*

„ 5. *Gallinæ*

Genera: *Didus, Pavo, Meleagris, Crax, Phasianus, Tetrao, Numida.*

„ 6. *Passeres*

Genera: (*a*) *Loxia, Fringilla, Emberiza;* (*b*) *Caprimulgus, Hirundo, Pipra;* (*c*) *Turdus, Ampelis, Tanagra, Muscicapa;* (*d*) *Parus, Motacilla, Alauda, Sturnus, Columba.*

Class III. Amphibia

Order 1. *Reptilia*

Genera: *Testudo, Draco, Lacerta, Rana.*

„ 2. *Serpentes*

Genera: *Crotalus, Boa, Coluber, Anguis, Amphisbæna, Cœcilia.*

Order 3. *Nantes*

Genera: *Petromyzon, Raja, Squalus, Chimæra, Lophius, Accipenser, Cyclopterus, Balistes, Ostracion, Tetrodon, Diodon, Centriscus, Syngnathus, Pegasus.*

Class IV. Pisces

Order 1. *Apodes*

Genera: *Murœna, Gymnotus, Trichurus, Anarrhichas, Ammodytes, Ophidium, Stromateus, Xiphias.*

,, 2. *Jugulares*

Genera: *Callionymus, Uranoscopus, Trachinus, Gadus, Blennius.*

,, 3. *Thoracici*

Genera: *Cepola, Echeneis, Coryphœna, Gobius, Cottus, Scorpœna, Zeus, Pleuronectes, Chœtodon, Sparus, Labrus, Scicena, Perca, Gasterosteus, Scomber, Mullus, Trigla.*

,, 4. *Abdominales*

Genera: *Cobitis, Amia, Silurus, Zeuthis, Loricaria, Salmo, Fistularia, Esox, Elops, Argentina, Atherina, Mugil, Mormyrus, Exocœtus, Polynemus, Clupea, Cyprinus.*

Class V. Insecta

Order 1. *Coleoptera*

Genera: (*a*) *Scarabaeus, Lucanus, Dermestes, Hister, Byrrhus, Gyrinus, Attelabus, Curculio, Silpha, Coccinella;* (*b*) *Bruchus, Cassida, Plinus, Chrysomela, Hispa, Meloe, Tenebrio, Lampyris, Mordella, Staphylinus;* (*c*) *Cerambyx, Leptura, Cantharis, Elater, Cicindela, Buprestis, Dytiscus, Carabus, Necydalis, Forficula.*

,, 2. *Hemiptera*

Genera: *Blatta, Mantis, Gryllus, Fulgora, Cicada, Notonecta, Nepa, Cimex, Aphis, Chermes, Coccus, Thrips.*

,, 3. *Lepidoptera*

Genera: *Papilio, Sphynx, Phalœna.*

,, 4. *Neuroptera*

Genera: *Libellula, Ephemera, Myrmeleon, Phryganea, Hemerobius, Panorpa, Raphidia.*

Order 5. *Hymenoptera*

Genera: *Cynips, Tenthredo, Sirex, Ichneumon, Sphex, Chrysis, Vespa, Apis, Formica, Mutilla.*

„ 6. *Diptera*

Genera: *Oestrus, Tipula, Musca, Tabanus, Culex, Empis, Conops, Asilus, Bombylius, Hippobosca.*

„ 7. *Aptera*

Genera: (*a*) Pedibus sex; capite a thorace discreta: *Lepisma, Podura, Termes, Pediculus, Pulex.*

(*b*) Pedibus 8–14; capite thoraceque unitis: *Acarus, Phalangium, Aranea, Scorpio, Cancer, Monoculus, Oniscus.*

(*c*) Pedibus pluribus; capite a thorace discreto: *Scolopendra, Julus.*

Class VI. VERMES

Order 1. *Intestina*

Genera: (*a*) Pertusa laterali poro: *Lumbricus, Sipunculus, Fasciola.*

(*b*) Imperforata poro laterali nullo: *Gordius, Ascaris, Hirudo, Myxine.*

„ 2. *Mollusca*

Genera: (*a*) Ore supero; basi se affigens: *Actinia Ascidia.*

(*b*) Ore antico; corpore pertuso laterali foraminulo: *Limax, Aplysia, Doris, Tethis.*

(*c*) Ore antico; corpore tentaculis antice cincto: *Holothuria, Terebella.*

(*d*) Ore antico; corpore brachiato: *Triton, Sepia, Clio, Lernæa, Scyllæa.*

(*e*) Ore antico; corpore pedato: *Aphrodita, Nereis.*

(*f*) Ore infero centrali: *Medusa, Asterias, Echinus.*

„ 3. *Testacea*

Genera: (*a*) Multivalvia: *Chiton, Lepas, Pholas.*

(*b*) Bivalvia (= *Conchæ*): *Mya, Solen,*

Tellina, Cardium, Mactra, Donax, Venus, Spondylus, Chama, Arca, Ostrea, Anomia, Mytilus, Pinna.

(*c*) Univalvia spira regulari (= *Cochleæ*): *Argonauta, Nautilus, Conus, Cypraæ, Bulla, Voluta, Buccinum, Strombus, Murex, Trochus, Turbo, Helix, Nerita, Haliotis.*

(*d*) Univalvia absque spira regulari: *Patella, Dentalium, Serpula, Teredo, Sabella.*

Order 4. *Lithophyta*

Genera: *Tubipora, Madrepora, Millepora, Cellepora.*

„ 5. *Zoophyta*

Genera: (*a*) Fixata: *Isis, Gorgonia, Alcyonium, Spongia, Flustra, Tubularia, Corallina, Sertularia, Vorticella.*

(*b*) Locomotiva: *Hydra, Pennatula, Tænia, Volvox, Furia, Chaos.*

The characters of the six classes are thus given by Linnæus :—

Cor biloculare, biauritum ; sanguine calido, rubro :
viviparis, *Mammalibus*
oviparis, *Avibus*
Cor uniloculare, uniauritum ; sanguine frigido, rubro :
pulmone arbitrario, *Amphibiis*
branchiis externis, *Piscibus*
Cor uniloculare, inauritum ; sanguine frigida, albida :
antennatis, *Insectis*
tentaculatis *Vermibus*

The Evolutionary Problem. In classifying animals on the basis of similarity of structure Linnæus in reality raised the essential issue around which centres the problem which we have formulated above. The evolutionary problem was really created by Linnæus, though he did not answer it in the way in which men of science would answer it to-day. Whatever may be said about the speculative discursions of some of the ancients, such

as Thales, who seem to have had some notion of an evolutionary process, no clear-cut issue existed, until the idea that like begets like, as a generalisation true for animals as a whole, was universally accepted. Immediately the Linnæan doctrine was established, speculation began, and from Lamarck till our own time the evolutionary idea has been an issue of intellectual importance.

Many of the steps which have led to the construction of this great generalisation of modern science are now of historical interest only. Without an understanding of the history of the theory of evolution, it is impossible to gain a clear idea of the position it occupies in scientific thought. In approaching it one has to remember that the discussion of organic evolution aroused a good deal of prejudice from theologians, and that in consequence many issues which were not strictly relevant to a straightforward presentation of the problem occupied a prominent place in the controversies that raged around it. Much of what was written on the evolutionary problem during the latter half of the last century was more concerned with disproving the doctrine of special creation than in developing the case for the theory of descent in as straightforward a manner as possible. In attempting to formulate the present status of the evolutionary hypothesis, we shall eliminate as far as possible these irrelevant questions, and deal only with the steps which have made a definite constructive contribution to the present state of knowledge. These will be treated under four headings :—

(*a*) The Principle of Biogenesis.
(*b*) The Law of Unity of Type.
(*c*) The Principle of Succession.
(*d*) The Principle of Genetic Variation.

Each of these principles deals with a different body of data, each involves the accumulation of a very large body of

observation, whose examination involved years of industry on the part of a large army of investigators, and therefore to avoid losing sight of the main issue in a mass of detail, it will be best to indicate in a general way what each of these contributions stands for in the history of the evolutionary theory.

(*a*) *The Principle of Biogenesis.* This is simply the doctrine that animals and plants arise only in our immediate experience from other animals and plants through the process of reproduction. It was accepted as generally true by Linnæus in his doctrine of the fixity of species with regard to animals in the ordinary sense. It was not until the middle of the nineteenth century that the work of Pasteur demonstrated its validity for micro-organisms.

(*b*) *The Law of Unity of Type.* This generalisation was the special contribution of the school of French and German comparative anatomists whose foremost exponent was Georges Cuvier (1829). The work of Linnæus gave a great impetus to the study of the structural differences between animals at a time when anatomy, like any young branch of knowledge, was still dominated by teleology, *i.e.* the belief that every phenomenon could be referred to some " purpose." The first classifications were based on comparatively superficial points of resemblance. As research progressed, it became evident that animals could be arranged in groups displaying a constellation of numerous structural characteristics involving a great variety of physiological units and that within such groups the greatest diversity of habitat could co-exist with this fundamental similarity of organisation. The underlying similarity of the bones of the limb and its musculature in a whale, a bird and an elephant, as contrasted with the limb structures of an insect, a fish or a squid, illustrate this conclusion. But the whole study of systematic zoology bears witness to it, and for that reason we shall have to make a survey of the animal kingdom from

the standpoint of systematic comparative anatomy. Von Baer extended the principle of Unity of Type to embryonic forms in 1834. The importance of the principle of Unity of Type to the rise of the Evolutionary Hypothesis lies in this fact, that by dismissing the teleological approach to the diversity of animal life, it paved the way for a naturalistic investigation of the problem.

(*c*) *The Principle of Succession.* When the Law of Unity of Type first obtained recognition, many fossils were known, but geologists had not arrived at a generally accepted view as to the order in which the various strata had been deposited nor the magnitude of the time which their formation occupied. By the middle of the nineteenth century the modern doctrine ("Uniformitarianism") had gained recognition. It then became apparent that, as we study the distribution of animals in space and time, we find that divergent forms which exist on the earth's surface to-day were preceded by widely distributed forms of a more generalised type in the past, so that the further we go back in the history of any group of animals, the less do we find the same pronounced differences as are displayed by existing members of the same assemblage. The differentiation of species is seen from the record of the rocks to have been a continuous process in space and time. This doctrine in its modern form was formulated in 1855 by Wallace.

(*d*) *The Principle of Genetical Variation.* Given the facts that animals only arise within our experience from other animals, that the diversity of animal life is not explicable as the expression of any supernatural arrangement of structure to meet the needs of environment, that the existing diversity of animal life has resulted from a gradual process of differentiation over long geological epochs, the proof that new forms, capable of transmitting to their progeny their own peculiarities, arise in our own immediate experience permits the conclusion that in the phenomenon of

genetical variation we have the means of interpreting the historic pageant of life as a material process.

Having laid down these principles, our next task will be to examine them in detail. The principle of biogenesis will first engage our attention. For purposes of reference a provisional scheme embodying the main groups of living organisms as recognised to-day is appended :—

A PROVISIONAL CLASSIFICATION OF ORGANISMS

A. PLANTS

B. PROTISTA
- Bacteria
- Cyanophyceæ
- Neosporidia
- Phytoflagellata
- Protozoa
- Mycetozoa, etc.

C. ANIMALS

Phylum	*Classes*
i. Porifera	
ii. Cœlenterata	Hydrozoa, Scyphozoa Actinozoa, Ctenophora
iii. Platyhelminthes	Turbellaria Trematoda, Cestoda Nemertinea [1]
iv. Nemathelminthes.	Nematoda Nematomorpha Acanthocephala
v. Rotifera (=Rotatoria=Trochelminthes)	
vi. Chætognatha.	
vii. Priapuloidea.	
viii. Sipunculoidea.	
ix. Polyzoa.	Ectoprocta Entoprocta, Phoronidea
x. Brachiopoda.	
xi. Echinodermata.	Echinoidea, Ophiuroidea Crinoidea, Asteroidea Holothuroidea
xii. Annelida.	Echiuroidea, Myzostomida Polychæta, Oligochæta Hirudinea

[1] The Nemertinea are often made a separate phylum.

Phylum	*Classes*
xiii. Mollusca.	Isopleura, Gastropoda
	Scaphopoda
	Pelecypoda (Lamelli-branchiata)
	Cephalopoda
xiv. Arthropoda.	Onychophora, Myriapoda
	Hexapoda, Trilobita
	Crustacea, Arachnida
xv. Prochordata.	Hemichorda, Tunicata
	Cephalochorda
xvi. Vertebrata.	Cyclostomes, Pisces
	Amphibia, Reptilia, Aves
	Mammalia

Chapter IX

THE PRINCIPLE OF BIOGENESIS

THE first step in the unfolding of the Evolutionary Argument, as we have indicated in the foregoing chapter, is concerned with the Principle of Biogenesis, or the fact that *like begets like*. Our knowledge of reproduction is quite a modern development. So commonplace a belief as that " like begets like " has only become a generally accepted doctrine since the labours of John Ray and Linnæus in the early half of the eighteenth century. Vergil's account of the manner in which a swarm of bees arise from the decomposing body of an ox represents an attitude of mind universal till that time.

Aristotle, who had a very extensive knowledge of the natural history of animals, a very detailed knowledge of the essential similarities in their anatomical characteristics, and a remarkably shrewd sense of their relative affinities, possessed very little knowledge of the reproductive processes. He recognised the principle that like begets like as applied to most Vertebrates and Molluscs (snails, clams, squids and their like) ; but even of a familiar animal such as the mouse his information was so scanty that he could write of its bearing several hundred offspring at a single birth. He refers to the belief that drone bees are produced from virgin eggs and queens from eggs after sexual congress ; but he discounts it, and evidently favours the belief that the workers at any rate are produced from the honey. Speaking of arthropods, he writes :—

Some of them are produced from similar animals, as phalangia and spiders from phalangia and spiders. . . . Others do not originate in animals of the same species, but their production is spontaneous, for some of them spring from the dew which falls from plants. . . . Some originate in rotten mud and dung. . . . Butterflies are produced from caterpillars and these originate in the leaves of green plants, especially the rhaphahus which some persons call crambe. . . . The gnats originate in ascarides (thread worms) and the ascarides originate in the mud of wells and running waters that flow over an earthy bottom. At first the decaying mud acquires a white colour, which afterwards becomes black, and finally red. . . .

FIG. 84—FIGURE OF THE BARNACLE AND GOOSE IN GERARD'S HERBALL (1594)

Such transformations were still the subject of current belief at the time of the Renaissance. The following passage from Gerard's *Herball* (1594) is representative of its time :—

But what our eyes have seene ; and hands have touched we shall declare. There is a small Island in Lancashire called the Pile of Foulders, wherein are found the broken pieces of old and bruised ships, some whereof have beene cast thither by shipwracke, and also the trunks and bodies with the branches of old and rotten trees, cast up there likewise, whereon is found a certain spume or froth that in time breedith unto certain shells, in shape like those of the Muskle, but sharper pointed, and of whitish colour, wherein is contained a thing in forme like lace of silke finely woven as it were together, of a whitish colour, one end whereof is fastened unto the inside of the shell, even as the fish of Oisters and Muskels are : the other end is made fast unto the belly of a

rude masse or lumpe, which in time commeth to the shape of a Bird ; when it is perfectly formed the shell gapeth open, and the first thing that appeareth is the foresaid lace or string ; next come the legs of the bird hanging out, and as it groweth greater it openeth the shell by degrees, til at length it is all come forth, and hangeth onely by the bill : in short space after it cometh to full maturitie and falleth into the sea, where it gathereth feathers, and groweth to a fowle bigger than a Mallard and less than a goose having blacke legs and bill or beak, and feathers blacke and white, spotted in such manner as is our magpie. . . . For the truth hereof if any doubt, may it please them to repaire unto me, and I shall satisfie them by the testimonie of good witnesses. . . . The bordes and rotten planks whereon are found these shels breeding the Barnakle are taken up on a small Island adjoyning Lancashire, halfe a mile from the main land, called the Pile of Foulders. They spawn as it were in March and April ; the Geese are formed in May and June, and come to fulnesse of feathers in the month after. And thus having through God's assistance discoursed somewhat at large of Grasses, Herbs, Shrubs, trees and Mosses, and certain Excrescences of the earth, with other things moe, incident to the historie thereof, we conclude and end our present Volume, with this Wonder of England. For the which God's Name be ever honoured and praised.

Much more might be added in the same vein. Writing shortly after the Renaissance period, Sir Thomas Browne states (*Vulgar Errors*, Book III) :—

Concerning the generation of frogs we shall briefly deliver that account which observation hath taught us. By frogs I understand not such, as arising from putrefaction, are bred without copulation and because they subsist not long are called temporariæ (Rana temporaria, the common frog), nor do I mean the little frog of an excellent parrot green that usually sits on trees and bushes, and is therefore called Ranuculus viridis (the tree frog), but hereby I understand the aquatile or water frog, whereof we may behold many millions every spring in England.

Referring to the doubt expressed by the author of *Vulgar Errors* with regard to Aristotle's belief that mice arise from

putrefaction, Alexander Ross (quoted by Parker) commented :—

So may one doubt whether in cheese and timber worms are generated ; or if beetles and wasps in cow's dung ; or if butterflies, locusts, grasshoppers, shell fish, snails, eels and such like be procreated of putrefied matter which is apt to receive the form of that creature to which it is by formative powers disposed. To question this is to question reason, sense, and experience. If he doubt of this let him go to Egypt, and there he will find the fields swarming with mice, begot of the mud of Nylus, to the great calamity of the inhabitants.

That canny Scot, Sir Robert Moray, perpetuated the mystery surrounding the reproductive habits of geese and barnacles so late as 1678 in the following words, which occur in a paper actually published in the Royal Society's Transactions : after describing the barnacle shells washed up on the coast of Scotland, he refers to their

little bill like that of a goose, the eyes marked, the head, neck, breast, wings, tail and feet formed, the feathers everywhere perfectly shaped and blackish coloured, and the feet like those of other water fowl to my best remembrance.

The name " goose barnacles " persists to this day.

Van Helmont (1577-1644) who occupies an honourable place not only in the history of physiology but equally in the history of chemistry, as the discoverer of carbon dioxide (gas silvestre), lent his authority to a time-honoured recipe for manufacturing mice by placing dirty linen along with a few grains of wheat or a piece of cheese in a closed receptacle. Redi's observations on the origin of maggots from blow-flies' eggs, like Valisneri's observations on the production of grubs in fruit, were in their time discoveries of a revolutionary character. Redi, an Italian, had shown (1668) that if flies are kept off meat by means of netting, the meat putrefies but no maggots appear in it. So hard was it to dispel the belief in spontaneous generation that Redi

himself regarded the insect larvæ in plant galls as the products of the plants themselves. "I do not consider it a great sin against philosophy," he wrote, "to maintain that the worms of plants are created by the same natural principle that produces the fruits of the plants."

Thus the belief in the species as a self-propagating unit was only generalised as the result of a long period of research covering more than two centuries after the work of the Renaissance biologists. So long as there existed a large number of *ad hoc* accounts for the origin of individual species the general problem of the origin of species could not emerge in its present form. Linnæus' doctrine of the fixity of species, if cast in a somewhat rigid mould, was nevertheless the foundation-stone of evolutionary biology. Though the species as a self-propagating unit became henceforth an axiom as applied to what are ordinarily called animals and plants, the doctrine of spontaneous generation lingered for a century after Linnæus in another field. It was not until the earlier part of the nineteenth century that the manufacture of high power achromatic microscopes permitted the detailed study of the life histories of those minute forms of life which are denoted by the term Protista. When we bear in mind the significance of the Principle of Biogenesis in the historical development of the Evolutionary Hypothesis it is not without interest that the revival of evolutionary speculation in the middle of the nineteenth century coincided with the culmination of the controversy which raged concerning the propagation of micro-organisms.

Micro-organisms. A brief reference to these is due before dealing with the final vindication of the Principle of Biogenesis through the work of Pasteur and Tyndall. The term *Protista* proposed by Haeckel (1834–1919) includes a various assemblage of minute forms of living matter, such as the bacteria. Some of the Protista have been customarily grouped together on account of

their active locomotion and absence of assimilatory pigments as *Protozoa* or primitive animals. Such are for instance Paramecium and the ciliary parasites like Opalina and Balantidium which abound in the rectum of the frog. Some Protozoa secrete shells of siliceous or calcareous material. They are respectively denoted by the terms Radiolaria and Foraminifera. Both of these have left abundant fossil remains, and the Foraminifera are largely responsible for the laying down of the chalk strata. Here also belongs a common object of the microfauna of muddy

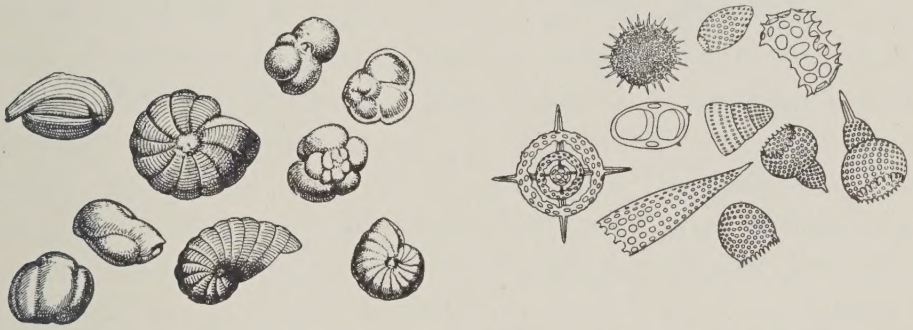

FIG. 85—SHELLS OF RADIOLARIA (right) AND FORAMINIFERA (left)

water, the *Amoeba* first described by Roesel of Nurnberg in 1755. Freshwater Amoebæ can usually be found in the muddy bottoms of ditches and ponds. They may attain a size just visible to the naked eye. Under the microscope they appear as masses of translucent granular material, the shape of which is constantly changing. The body substance or *protoplasm* is constantly flowing out in processes called *pseudopodia*. As new pseudopodia are formed old ones are withdrawn, and by this streaming out of the cell substance Amoeba both creeps over the surface to which it is attached and engulfs the food which it is constantly taking in. This food consists of smaller organisms and organic débris. Amoeba reproduces like Paramecium by binary fission. This process involves the division of a structure

within the body substance which stains like the nucleus of the cells of animal bodies, and behaves in division like a nucleus. In short, Amoeba is essentially like one of the colourless cells in the blood of the frog or Man. The white blood corpuscle is, however, part of a whole animal, whereas Amoeba is a complete independent organism. Many writers speak of the Protozoa as unicellular organisms on this account. It is more logical, as Dobell has pointed out, to refer to them as non-cellular, since the term cell was first given to the parts of a whole plant or animal.

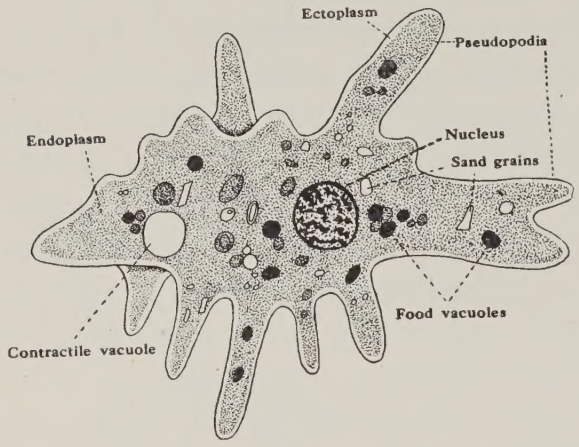

FIG. 86—A PROTEUS AMOEBA (greatly magnified)

The Protista then are non-cellular organisms, that is to say, their bodies are not divided up into cells. Naturally a clear appreciation of their structure did not emerge until after the Cell Theory of Schleiden and Schwann (1834–39) had been established. The comparison between the body of a Protozoan and a cell of the body of a typical animal or plant was first made by Barry (1843) and von Siebold (1845). Up till that time Protista had been classified under the term Infusoria (now retained for the ciliate Protozoa only) along with a number of minute organisms, among which may be mentioned the Rotifera, or wheel animalcules, which abound in fresh water. The Rotifers, first seen by Leeuwenhoek (1677) who also described numerous Protozoa, are, in spite of their small size, animals of fairly complex organisation, with tissues and organs formed of separate cells. Till the advent of the Cell doctrine there were numerous biologists

who attributed to the Protozoa an elaboration of internal organs analogous to those of a typical animal.

"*Spontaneous Generation.*" Controversy concerning the propagation of the Protista continued from their discovery by Leeuwenhoek until nearly the end of the nineteenth century. In 1718 Joblot showed that hay infusions can be sterilised by boiling against infection with Infusoria. From 1765 onwards, in a series of researches, Spallanzani continued this work, improving the technique of Joblot by boiling his cultures in hermetically sealed flasks, so that the surrounding air was sterilised. On the basis of his experiments Spallanzani asserted the doctrine of Biogenesis as applicable to the micro-organisms. But the study of minuter forms of life—the bacteria—after the improvements of microscopic apparatus in the first half of the nineteenth century re-opened the question. For while better microscopic equipment permitted more detailed study of the life histories of the Protozoa and thus firmly established the principle that like begets like for the Infusoria, it led to the recognition of smaller organisms which are far more resistant to heat.

Pasteur's name has pre-eminence in connection with the identification of the bacteria as the agents of putrefactive processes, and it was his work which first placed on a firm basis the universal truth of the doctrine of Biogenesis. The reality of spontaneous generation was reaffirmed by a French zoologist Pouchet, in 1858, in a paper communicated to the Académie des Sciences under the title "Note on Vegetable and Animal proto-organisms spontaneously generated in artificial air and oxygen gas." In a series of researches published in the three succeeding years Pasteur took up the challenge. Pasteur began by the microscopic study of atmospheric air. He passed air continuously through plugs of cotton wool, and showed that by adding the deposited dust to sterile media, cultures of bacteria

could be obtained. He then showed that the most putrescible fluids remained uninfected if kept out of range of atmospheric dusts. After Pasteur's work the question was again re-opened by Bastian during the seventies. Bastian in particular dwelt upon the fact that mere boiling for short periods does not suffice to destroy all bacterial organisms, but the later investigations of Tyndall and of Dallinger and Drysdale led to the recognition of stages in the life cycle of bacteria that are more resistant to heat than is the motile form. Since that time the issue has not been raised. The possibility that ultra-microscopic organisms are spontaneously generated is not absolutely disproved, but there is no reason to believe in it.

The recognition of the Principle of Biogenesis conditioned the formulation of the Evolutionary problem by disposing of a large nexus of *ad hoc* hypotheses to account for the origin of individual species. It had an even greater significance, for it pointed the way to further analysis of the origin of species. By showing that all individuals of a species are genetically continuous, that is to say, are connected by the tie of common descent, it necessitated the consideration of the possibility that individuals of the larger units of classification (genera, orders, classes) are likewise of common genetic origin. Thus the Principle of Biogenesis may be taken as the first step in the development of the evolutionary argument.

Chapter X

THE PRINCIPLE OF UNITY OF TYPE [1]

ARISTOTLE borrowed from Plato the view that interprets phenomena in relation to some pre-ordained end. This aspect of Aristotle's teaching rather than the fact-loving temper of the *History of Animals* was prominent in the philosophical schools of the Middle Ages. Differences and similarities of anatomical structure came to be exclusively attributed to special design. Like the Aristotelian belief in spontaneous generation, this view obstructed further progress in the development of an evolutionary interpretation of the species problem.

As the study of animal structure progressed in the two generations that followed the labours of Ray and Linnæus, it became increasingly evident that the teleological view of animal structure was an inadequate one. In the field of animal behaviour this point of view lingered on till the middle of the nineteenth century, as the concluding remarks of the article on Instinct in the eighth edition of the *Encyclopædia Britannica* show :—

> It thus only remains for us to regard instinct as a mental faculty *sui generis*, the gift of God to the lower animals, that man in his own person, and by them, might be relieved from the meanest drudgery of nature.

[1] The subject matter treated in this chapter is intended to be supplemented by laboratory dissections of Invertebrates, as directed in Gilchrist and von Bonde's practical manual, and by field work and museum study with the use of some standard work such as Parker and Haswell, Shipley and MacBride or Sedgwick for further reference.

If animals had been specially designed to suit their conditions of life, it would be expected that the greatest degree of similarity would exist between animals pursuing a similar mode of existence. Actually we find nothing of the sort. On the contrary, as we make the greatest degree of similarity in structure the basis of our attempts to classify animals, our units of classification resolve themselves into collections of forms which show the greatest diversity of habit, locality, diet, means of progression or anything else to which a teleological significance might be attributed. We find that animals can be classified in groups based on a striking similarity in architecture and development with regard to complex constellations of physiological units. Within these groups the utmost variety of habitat, climate, locomotion, nutrition, etc., are encountered.

Comparison of Vertebrate and Arthropod. To illustrate this conclusion three types of Vertebrates and three representatives of the Arthropod phylum will serve. In these two groups the greatest activity and complexity of behaviour is attained. The types we shall select are respectively characterised by an aerial, an aquatic, and a terrestrial method of existence. From the phylum Vertebrata it will be convenient to select the pigeon (*Columba livia*) as an aerial type, the dogfish (*Scyliorhinus canicula*) as an aquatic type, and the frog or the rabbit (*Lepus cuniculus*) as a terrestrial type. As an aerial Arthropod, an insect, the cockroach (two species, *Periplaneta orientalis* and *Periplaneta americana* are common) is suitable because of its size and general availability, although immature individuals and the females of *P. orientalis* are wingless. As an aquatic Arthropod we shall take one of the larger crustaceans, such as the crayfish (*Astacus fluviatilis*) or the lobster (*Homarus vulgaris*). As a terrestrial flightless Arthropod we select an Arachnid, the scorpion, because of its size ; the species shewn in Fig. 88 is

the South African *Uroplectes insignis*, but any of the true scorpions, of which preserved specimens are easily obtainable, will serve.

Let us take to begin with the characteristic responses of these two sets of types. The most obvious form of response is muscular activity. Now if we take the wing of the pigeon, the pectoral fin of the dogfish or the fore leg of the frog or rabbit, we find in all cases that the innermost core

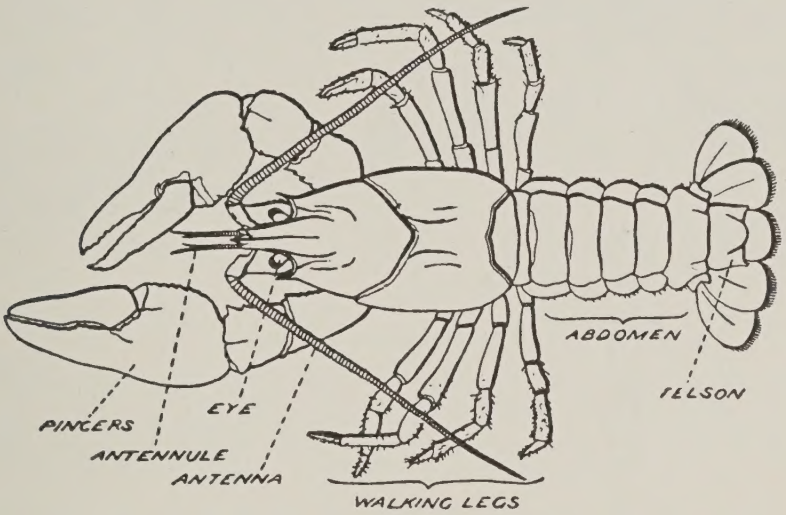

FIG. 87—THE CRAYFISH

of the limb is a hard, jointed structure made of bone or cartilage. To these jointed skeletal elements the muscles are attached. The muscles lie superficial to the joints; and the limb is not externally divided into clearly marked-off segments. The same remarks apply to the hind limbs of all three types and to the tail of the dogfish, which is its chief organ of propulsion. With the three Arthropod types the relation of the muscles to the hard parts is quite different. If we examine the walking legs of the cockroach, the crayfish or the scorpion, we find that in each case the limb is externally hard and divided into very distinct segments. On cutting through the hard tubular wall of a limb, we find the

muscles within the tube attached at one end to inward projections of one segment and to the internal wall of another segment at the other (Fig. 11). The wing of the cockroach is attached at its base to muscles which pass in an analogous manner to the inner ventral surface of the hard wall of the thorax.

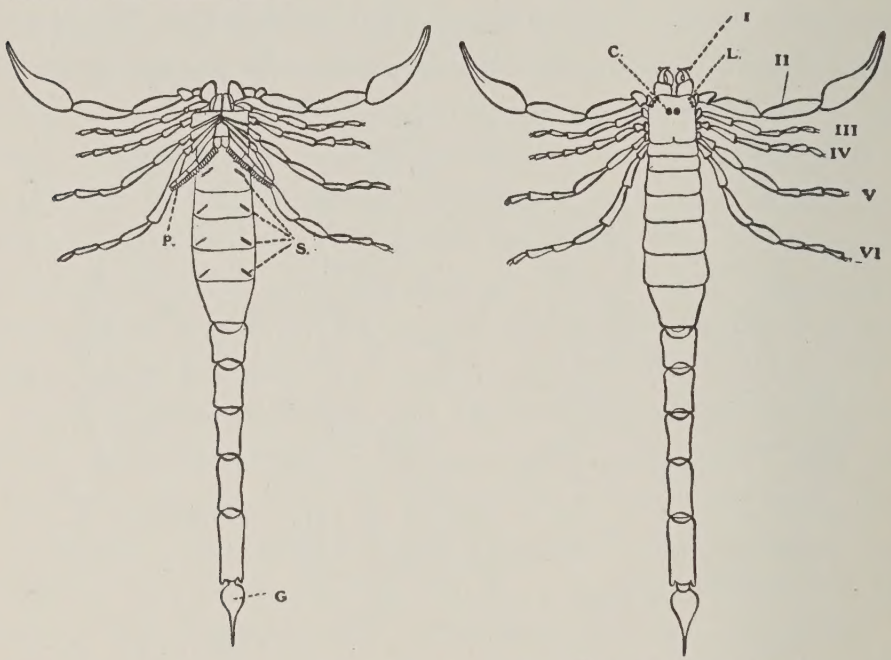

FIG. 88—THE CAPE SCORPION (*Uroplectes insignis*)

I–VI—Appendages. L—Lateral eyes (3 pairs). C—Compound eyes. P—Comb-like abdominal appendages or *pectines*. S—Openings of book lungs. G—Sting.

In the three Arthropod types we are considering, the trunk, like the limbs, is also segmented, and powerful extensor and flexor muscles attached to the hard outer shell of the body control its movements in a manner analogous to that already seen in the jointed limbs. The latter include, in addition to the walking legs, other " appendages " used in various activities. In the crayfish there are nineteen pairs of appendages, thirteen being attached to the anterior unsegmented part of the body—the cephalothorax—and six to the six segments of the abdomen. The two most anterior pairs of appendages are feelers or antennæ ; then follow a series just behind the

mouth, and these are employed in seizing and masticating the food, the most anterior, or mandibles, having powerful cutting bases. Behind these, but still on the cephalothorax, come five pairs of walking legs, of which the foremost end in the conspicuous pincers. The abdominal appendages are mostly two-branched or biramous, and are used in swimming or serve for the attachment and aeration of the eggs in the female. But the first two pairs of abdominal appendages are exceptional; in the male they are employed for

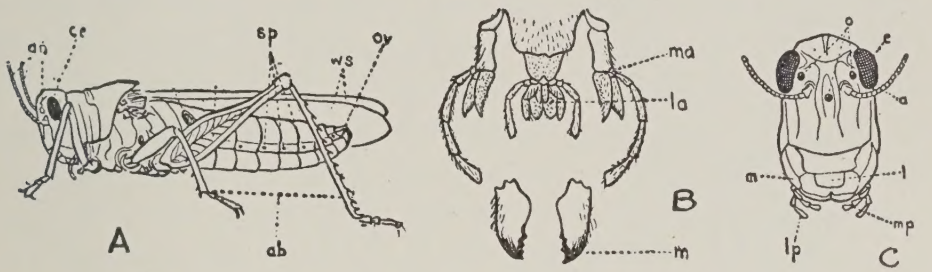

FIG. 89—THE LOCUST

(A) A typical insect; showing also mouth parts (B); and head (C). *o*—ocelli or simple eyes; *ce* or *c*—compound eyes; *an* or *a*—antennæ; *m*—mandibles; *ma*—first maxilla; *la*—second maxilla or labium; *l*—upper lip or labrum; *mp*—palps or limb-like part of the maxillæ; *lp*—palps of the labium; *sp*—spiracles or stigmata, the external apertures of the tracheal system; *ov*—ovipositor.

transferring seminal fluid to the female, while in the latter they are small or absent. The cockroach has in addition to three pairs of walking legs a single pair of antennæ and three pairs of masticatory appendages, one of which, the mandibles, have cutting bases. The head appendages of the locust in Fig. 89 are essentially similar to those of the cockroach. The abdominal segments do not carry limbs, but some wingless insects like the minute white Campodea have small inconspicuous appendages—probably quite useless—attached to the abdominal segments. The scorpion, like the spider and tick, is a blood sucker, and has neither feelers nor masticatory mandibles like those of the cockroach or crayfish, but there are two pair of appendages in front of the walking legs, the large pincers or pedipalps, used to seize the prey, and in front of the mouth a three-jointed

pair, the cheliceræ, by which the animal attaches itself to the part from which it sucks the juices of its victim. Behind the last walking legs, of which there are four pairs, in contradistinction to the crayfish, which has five, and the insect, which has three, there is in the scorpion a pair of comb-like appendages (pectines) whose precise significance, if any, is not known.

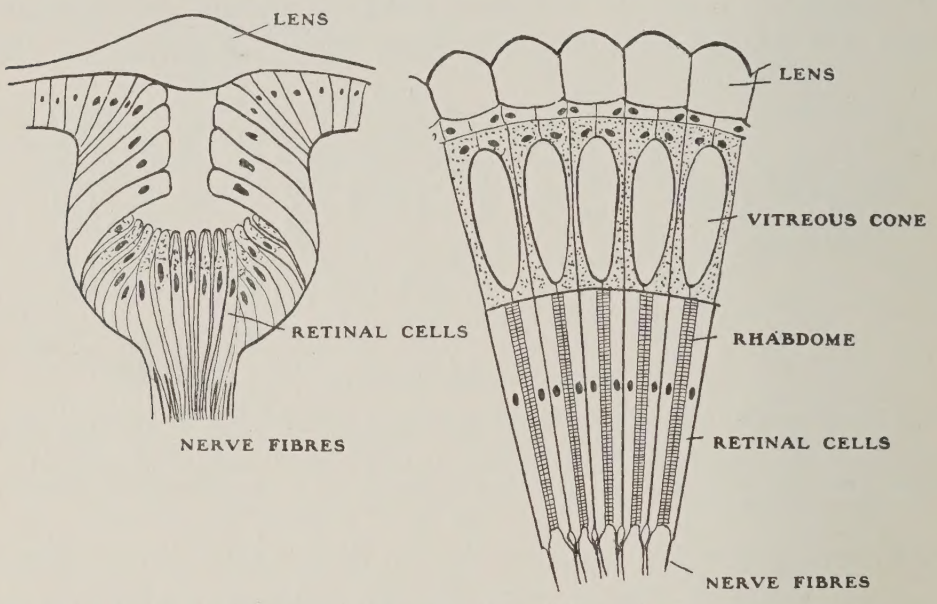

FIG. 90—EYES OF ARTHROPODS

On left, simple eye ; on right, part of a compound eye. Both are in vertical section.

Bodily movement in the insect, as we have noted, is very considerably influenced by light, and it is the light receptor which usually shows the greatest structural complexity of any of the receptor organs. In the case of our Vertebrate types, the description of the eye already given—cornea, iris, lens, aqueous and vitreous humour, retina (p. 40)—applies to each. In all three cases, moreover, the eye is movable within its orbit by the action of six very characteristically arranged eye muscles. In all three cases the retinal part of the eye arises in the embryo as an outgrowth from the brain. In the case of the scorpion

there are two sets of eyes. There are three pairs of small eyes on either side at the anterior extremity, called the lateral eyes, and there is a single larger pair on the centre of the carapace. The lateral (*simple*) eyes consist of a biconvex thickening of the transparent cuticle lying over a group of photosensitive cells which are the specialised endings of afferent fibres running back to the brain. In the case of the central eyes these photosensitive cells are arranged in groups of about six around a central vitreous rod secreted by them, and separated from adjacent groups by a thin layer of pigmented connective tissue cells. This subdivision of the retinal part of the eye into separate " retinulæ " is carried still further in the large *compound eyes* of the crayfish and the cockroach, in which the surface of the cuticle is divided into a number of separate facets. Between each facet and its underlying group of retinal cells there is an additional refractive " vitreous cone " secreted by a special group of cells which surround it. There is no sharp line of demarcation between the extremely simple lateral eyes of the scorpion and the compound eyes (Fig. 90) possessed by most of the phylum Arthropoda in which the scorpion, the cockroach, and the crayfish are placed. Indeed, in some insects there are on the front of the head small eyes which are of the same type as the lateral eyes of the scorpion. Moreover, although many adult insects (such as the cockroach) do not possess these accessory simple eyes, the eyes of insect larvæ are of the simple type. Incidentally, it may here be mentioned that there is in the Vertebrate body a structure of somewhat the same type as some of the simpler eyes of Arthropods, namely, the pineal eye of the New Zealand lizard and the lamprey larva. In all Vertebrates there is a median glandular body, the pineal gland, attached by a stalk to the posterior part of the dorsal surface of the fore brain. Its rôle in the animal economy is unknown. In some reptiles it lies outside a small foramen in the top of the skull immediately beneath

the epidermis, and such foramina are common in the skull of fossil reptiles and amphibia. In a few forms, such as those mentioned above, it has a structure very much like the eye of many invertebrates. That it is a truly photoreceptive structure in any animal, however, is not experimentally established. From the embryological standpoint the Vertebrate eye differs from any Arthropod eye, in that the retina is developed as a cup-like outgrowth of the brain, which meets the cellular lens formed from the outer skin. The retinal elements of the Arthropod eye grow inwards in development to join the brain.

We next consider the linking up of the receptor and the effector, the apparatus of reflex response. In all the animals we are dealing with this involves the transmission of a nervous impulse through at *least* two fibres, one conveying it to a part of the concentrated mass of nervous tissue called the central nervous system, and one passing out from the C.N.S. by way of a nerve fibre whose cell body is present in the C.N.S. itself. In all cases the central nervous system itself is clearly demarcated into regions where the nerve cells are congregated, and regions composed exclusively of fibres running from one segment to another. In all cases there is a special concentration of nervous tissue at the anterior extremity of the body, where the mouth and eyes are located. But here the similarity ends. In the three Vertebrate types we have taken, the afferent fibre has its cell body (except in the case of the olfactory and optic nerves) in a ganglion close to the junction of the nerve with the C.N.S. In the three Arthropod types the afferent nerve has its cell body on the receptive surface. In the vertebrate types most of the large nerves are connected with the C.N.S. by separate afferent and efferent roots. In the Arthropod types this is not the case. In the Vertebrate types the C.N.S. arises as a tubular infolding of the outer skin of the embryo along the mid-dorsal line, and is wholly

dorsal to the alimentary canal. In the three Arthropod types the central nervous system (Fig. 93) lies above the alimentary canal at the anterior extremity only (brain or supraœsophageal ganglia). This part is connected by fine strands with a double cord composed of alternate thick portions (ganglia) and thin portions below the alimentary canal. In this type of C.N.S. the regions in which nerve cells and fibres occur alternate with one another, a ganglion, or more strictly a pair of ganglia, being typically present in each segment, whereas in the Vertebrate C.N.S. the connecting fibres lie outside (white matter) the regions where nerve cells (grey matter) occur in the spinal cord.

If we now turn to those structures which are specially concerned with the distribution of the materials from which the energy of reflex response is derived, we see equally striking differences between the three Vertebrate and the three Arthropod types. In all the Vertebrate types we find three very characteristic sets of digestive glands manufacturing the same type of secretions—the gastric glands, the liver with its gall bladder and the pancreas. There is no such close similarity in the digestive system of the three Arthropod types, but we may note in all of them a feature which distinguishes them sharply from the Vertebrate types: for some length inwards both the hind gut and the fore gut are lined by a thin coat of chitin, the material of which the hard outer wall of the body is formed. The Vertebrates have in their blood a red, iron-containing pigment, Hæmoglobin, which is carried by special blood cells and by combining reversibly with oxygen acts as the vehicle by which the latter is transported. In the Arthropods this function is generally performed by the quite different pigment Hæmocyanin, which is pale blue when oxidised, and contains copper instead of iron. Reduced hæmocyanin is colourless. Moreover, in the circulatory organs of the Arthropod types we find an entirely unique arrangement. There is a large

muscular heart lying above the alimentary canal. This heart (Fig. 93), has a paired series of valvular apertures known as ostia on either side of it. The heart pumps blood out to the tissues by arteries which are chiefly derived from two main trunks from the anterior and posterior end of the heart respectively. Thence the blood percolates into the tissue spaces which communicate ultimately with the body cavity in which the heart lies. The body cavity in which the organs

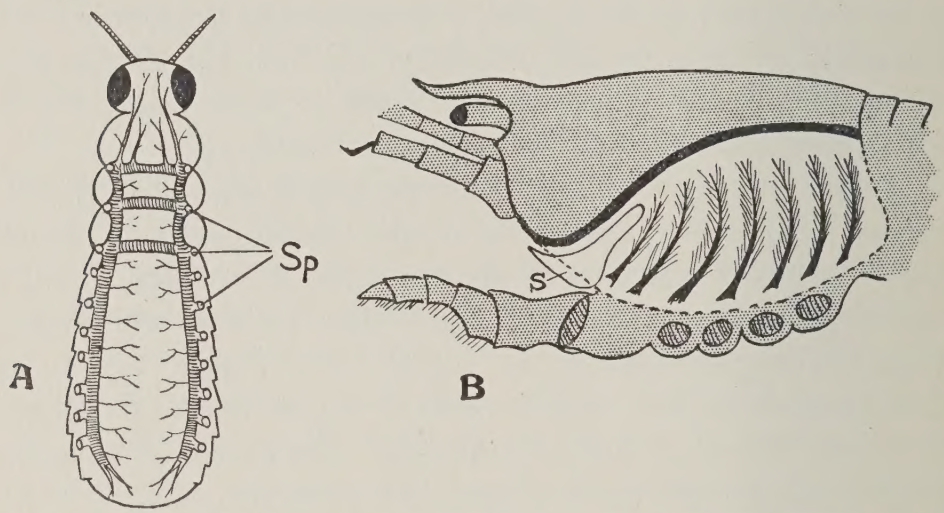

FIG. 91—GROSS ANATOMY OF RESPIRATORY ORGANS OF ARTHROPODS

A—The larger tracheæ of an insect; Sp—Spiracles. B—The gill chamber of a large Crustacean, opened from the side; s—The baler or scaphognathite.

lie is a blood space, and the heart fills itself at each beat from the surrounding fluid which enters it via the ostia. The Vertebrate circulation, on the other hand, is a closed system of vessels, which presents certain universal features within the group even in the adult, notably the important fact that the blood from the capillary bed of the alimentary canal passes via the hepatic portal vein to the liver, through whose capillaries it must pass on its way back to the heart.

It is true that there are striking differences between the circulatory systems of land and water vertebrates. But the main plan of the arterial system in all is essentially similar at an early stage of development. This we have

studied already (p. 98) and have noted its relation to the methods of respiration that exist in different types of Vertebrates. No such extreme differences are correlated with the different methods of breathing which occur in different Arthropods (Figs. 91 and 92). But it may be noted that in the insects generally the heart is very thin and the arterial system practically non-existent. Now in the insect there is a system of fine tubes lined by thin cuticle with annular thickenings. These tubes are known as tracheæ. These tracheæ ramify throughout the entire body, ending blindly in the deepest tissues. They communicate by paired apertures (spiracles or stigmata) on either side of

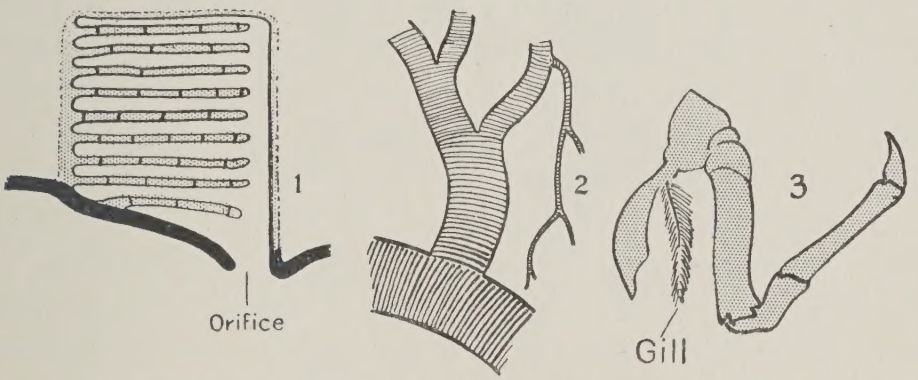

FIG. 92—RESPIRATORY STRUCTURES OF ARTHROPODS

1—Microscopic section through book lung of scorpion; 2—Microscopic appearance of a trachea from an insect; 3—Walking leg of a lobster with gill attached.

the body, and air is kept in circulation by rhythmical movements of the abdomen that can be easily observed in a cockroach or locust. The oxygen content of the tracheæ goes down during activity, and the carbon dioxide production goes up. If we block the spiracles the oxygen intake of an insect falls to a small fraction of its normal dimensions. Thus oxygen is brought to the tissues directly in insects. Tracheæ are also found in centipedes and millipedes, spiders and ticks. They do not occur in scorpions or in the crayfish. The third, fourth, fifth and sixth abdominal segments in the scorpion have each a

pair of slit-like apertures on the ventral surface. These slits lead into sacs called book lungs, on account of the fact that the internal wall (Fig. 92) is thrown into plate-

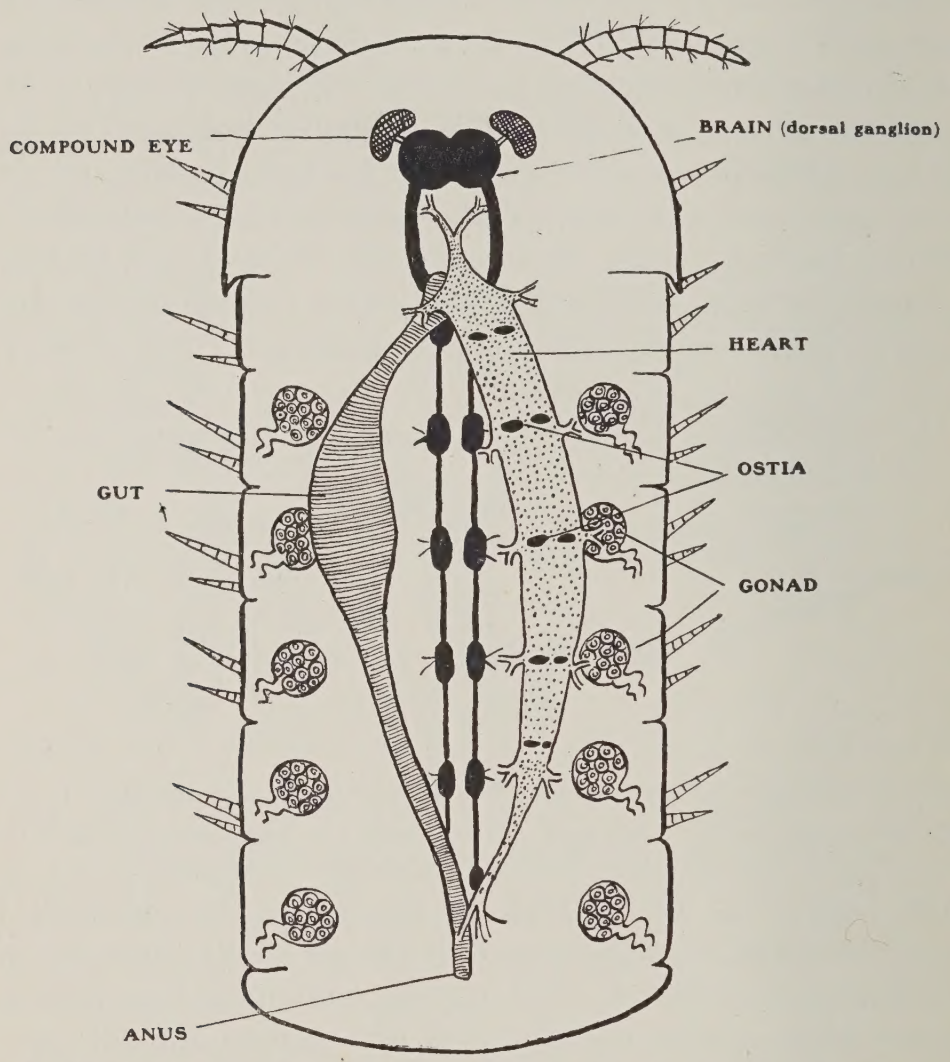

FIG. 93—DIAGRAMMATIC REPRESENTATION OF AN IDEAL ARTHROPOD

like projections overlapping like the leaves of a book. They offer a large surface for the diffusion of respiratory gases. Experiment shows that on occluding the apertures of the book lungs the oxygen consumption of the scorpion is very greatly reduced, so that they are actually the main

seat of oxygen intake, like our own lungs. The crayfish has respiratory organs of another type. Superficial examination reveals a large space between the bases of the legs and a downward projection of the dorsal wall of the cephalothorax on either side. These lateral gill chambers, as they may be called, are open to the exterior by fairly wide apertures at the sides of the mouth. The cavity of the chamber is largely taken up by tufts of fine filaments springing from the bases of the legs and resembling a test tube brush in arrangement. These are the "gills." Water is kept constantly circulating over them by the incessant rhythmical motion of a plate-like extension of the base of the third masticatory appendage (second maxilla) which constitutes a baler, sometimes referred to by the technical term scaphognathite. If the baler is removed the oxygen consumption of the animal immediately sinks to negligible proportions. So we may conclude that the main surface for diffusion of oxygen from the water into the body is provided by the gill filaments.

Summarising, then, our survey of the physiological anatomy of terrestrial, aquatic and aerial Vertebrates, and terrestrial, aquatic and aerial Arthropods, we see in every aspect of structure certain clear features of similarity which the terrestrial Arthropod shares with the aerial or aquatic Arthropod, and does not share with the terrestrial Vertebrate. We see in every aspect of structure certain features which the aerial Vertebrate shares with an aquatic Vertebrate or a terrestrial Vertebrate, but does not share with an aerial Arthropod. On this basis we are justified in grouping the three Vertebrate types and the three Arthropod types in two separate assemblages based on underlying similarity independent of any teleological implication, and we are thus led to shoulder the task of seeking for some non-teleological interpretation of the similarities which animals display.

Classification of the Vertebrate and Arthropod phyla. Before proceeding further with this theme it would be

appropriate to insert a few words about the diversity of forms met with in the new phylum to which we have been introduced, and to define the present limits of the group. The Arthropoda may be defined as: Segmented animals in which the nervous system has the same relations as in segmented worms (*vide infra*), *i.e.* a large pair of ganglia situated dorsally in the preoral segment, and connected on either side with a double chain of ganglia more or less approximated ventrally beneath the alimentary canal. The body cavity, however, is a blood space which communicates with the dorsal median heart by paired valvular ostia. With the single exception of the aberrant genus,

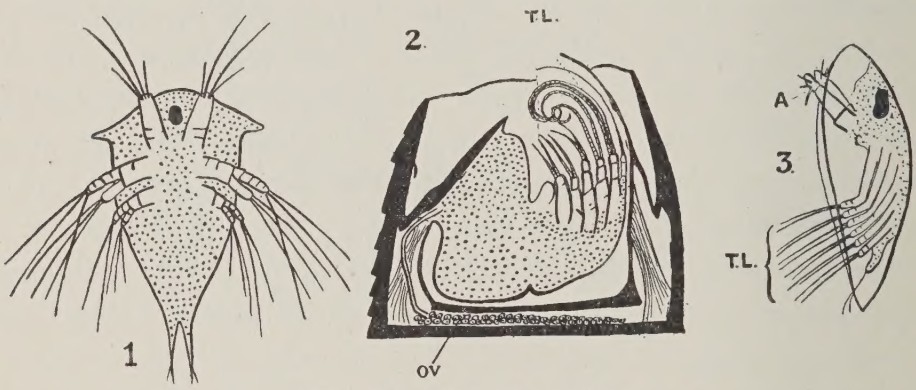

FIG. 94—THE BARNACLE

1—The Nauplius or first larval phase with median eye and three pairs of bi-ramous appendages, characteristic of the larvae of many orders of Crustacea; 2—Vertical section through whole adult showing shell, plates and six pairs of biramous jointed thoracic limbs (T.L.); 3—The Cypris or second larval phase which has in addition to the antennæ (A) and masticatory appendages, six pairs of biramous swimming limbs (T.L.)

Peripatus, they have jointed limbs with separate muscles. The group may be divided into the following classes:—

1. *Trilobita* (primitive and exclusively fossil)—Segments are alike bearing biramous (two-branched) appendages with masticatory bases, except the preoral pair which are antenniform.

2. *Onychophora*—Body unsegmented externally, and the limbs, which are all alike except the antennæ and mandibles, are not jointed. Diffuse tracheal system. There are coelomic ducts, thought to be excretory tubules, in every segment. *e.g.* Peripatus.

3. *Crustacea*—These resemble trilobites most closely. Some segments bear biramous appendages. They have two pairs of antennæ and mandibles and are mostly marine. *e.g.* shrimps, lobsters, crabs, wood lice, pill bugs, water fleas.

4. *Arachnida*—No antennæ, no mandibles. Six or seven pairs of appendages in front of the genital orifice. The first pair are typically chelate and are called cheliceræ. At least four of the remaining pairs are walking legs. *e.g.* king crabs, scorpions, spiders, mites and ticks.

5. *Insecta* (*Hexapoda*)—One pair of antennæ and mandibles. Three pairs of walking legs. *e.g.* bugs, flies, beetles, wasps and bees, butterflies, termites.

6. *Myriapoda*—One pair of antennæ and mandibles. All segments behind the head alike and bear walking legs. *e.g.* centipedes and millipedes.

At the same time, we may pause to define the different classes into which the Vertebrate phylum is customarily divided at the present time. There are five principal classes ; and an additional group, the Cyclostomes, which in their general organisation resemble the fishes in most essentials, *e.g.* their circulatory system is of the Piscine type, but they are separated on account of the absence of any trace of jaws or limb structures.

A. Without Limbs or Jaws
(i) *Cyclostomes* (Lampreys and hagfish)

B. With Fins supported by Fin Rays
(ii) *Pisces* (true fishes)

C. With Five-fingered Limbs
(1) With functional aquatic respiration at some stage and undivided ventricle ; no bony chest
(iii) *Amphibia* (frogs, toads, salamanders)

(2) No aquatic respiration :
(*a*) Ventricle incompletely divided, two aortic arches, external covering of scales
(iv) *Reptilia* (lizards, tortoises, crocodiles, snakes).
(*b*) Right aortic arch only persists ; external covering of feathers
(v) *Aves* (birds).

(*c*) Left aortic arch only persists; muscular diaphragm; three ear ossicles; external covering of hair

(vi) *Mammalia* (kangaroo, bat, whale, dog, horse, rabbit, man)

Classifications of Lamarck and Cuvier. A very fundamental similarity thus exists between the representatives of three great classes of Vertebrates, on the one hand, and three representatives of what we now call Arthropods on the other. The recognition of this unity is foreshadowed in the classification of animals given by Lamarck (1808) fifty years after the publication of the *Systema Naturæ*. Lamarck departs so far from the anthropocentric point of view of Linnæus as to create a major assemblage, the Vertebrata, to include the four first classes of Linnæus' six divisions of the animal kingdom. Lamarck also split up Linnæus' order Insecta and adopted the two classes Arachnida and Crustacea, from which we have selected two of the types discussed above, but he included in the Arachnida a certain number of what are to-day regarded as wingless insects and the centipedes and millipedes. Below is given the classification of Lamarck:—

A. Invertebrata

1. "Apathetic" animals
   - Class I. Infusoria
   - Class II. Polypi (this includes Hydroids, Rotifera, Polyzoa, some Echinoderms)
   - Class III. Radiaria (jellyfishes, sea anemones, starfishes and sea urchins)
   - Class IV. Tunicata (present group)
   - Class V. Vermes (non-segmented worms)

2. "Sensitive" animals
   - Class VI. Insecta (Linnæan orders maintained)
   - Class VII. Arachnida
   - Class VIII. Crustacea
   - Class IX. Annelida (segmented worms)
   - Class X. Cirripedia (barnacles)

Class XI. Conchifera (clams)
Class XII. Mollusca
Orders ; Pteropoda ; Gastropoda, Cephalopoda, Heteropoda, Trachelipoda

B. VERTEBRATA. "Intelligent" animals
Class XIII. Pisces
Class XIV. Reptilia (= Linnæus' "Amphibia")
Class XV. Aves
Class XVI. Mammalia

Here we see the introduction of many terms that have been incorporated in modern schemes of classification. The outstanding positive feature is the recognition of unity of type within the Vertebrate series. Linnæus' treatment of Vertebrate animals had been correlated very largely with habit of life, though it is true that the principle of unity of type is already emergent in his recognition of the bats and whales as mammals. Lamarck on the other hand, while correctly recognising the heterogeneity of Linnæus' "Insecta," fails to grasp the fundamental similarity of the three great classes of Arthropods which he now denotes by the terms "Insecta," "Arachnida" and "Crustacea." A more explicit attempt to express the principle of Unity of Type is seen in the classification put forward in Cuvier's *Le Regne Animal* (1829). This was as follows :—

FIRST BRANCH : ANIMALIA VERTEBRATA

Class I. MAMMALIA
Orders : *Bimana, Quadrumana, Carnivora, Marsupialia, Rodentia, Edentata, Pachydermata, Ruminantia, Cetacea*

Class II. BIRDS
Orders : *Accipitres, Passeres, Scansores, Gallinæ, Grallæ, Palmipedes*

Class III. REPTILIA
Orders : *Chelonia, Sauria, Ophidia, Batrachia*

Class IV. FISHES
Orders : (*a*) *Acanthopterygii, Abdominales, Subbrachi, Apodes, Lophobranchii, Plectognatha ;* (*b*) *Sturiones, Selachii, Cyclostomi*

SECOND BRANCH: ANIMALIA MOLLUSCA

Class I. Cephalopoda

Class II. Pteropoda

Class III. Gastropoda
Orders: *Pulmonata, Nudibranchia, Inferobranchia, Heteropoda, Pectinibranchia, Tubulibranchia, Scutibranchia, Cyclobranchia*

Class IV. Acephala
Orders: *Testacea, Tunicata*

Class V. Brachiopoda

Class VI. Cirrhopoda

THIRD BRANCH: ANIMALIA ARTICULATA

Class I. Annelides
Orders: *Tubicolæ, Dorsibranchiæ, Abranchiæ*

Class II. Crustacea
Orders: (*a*) Malacostraca: *Decapoda, Stomapoda, Amphipoda, Lœmodipoda, Isopoda;* (*b*) Entomostraca: *Branchiopoda, Pœcilopoda, Trilobitæ*

Class III. Arachnides
Orders: *Pulmonariæ, Trachearіæ*

Class IV. Insecta
Orders: *Myriapoda, Thysanura, Parasita, Suctoria, Coleoptera, Orthoptera, Hemiptera, Neuroptera, Hymenoptera, Lepidoptera, Rhipiptera, Diptera*

FOURTH BRANCH: ANIMALIA RADIATA

Class I. Echinoderms
Orders: *Pedicellata, Apoda*

Class II. Intestinal Worms
Orders: *Nematoidea, Parenchymatosa*

Class III. Acalephæ
Orders: *Simplices, Hydrostaticæ*

Class IV. Polypi (including the *Cœlenterata* of modern authorities and the *Polyzoa*)
Orders: *Carnosi, Gelatinosi, Polypiarii*

Class V. INFUSORIA

Orders: *Rotifera, Homogenea* (this includes the *Protozoa* of recent writers and *Protophyta*)

The Mollusca. This scheme abandons the anthropocentric standpoint implicit in the work of Lamarck as well as in that of Linnæus, inasmuch as the former classified animals in a "Scala Naturæ" leading up to Man at its summit. It envisaged the animal kingdom as divisible into four independent assemblages each with its own underlying unity of type. It adopts as three of its four major divisions

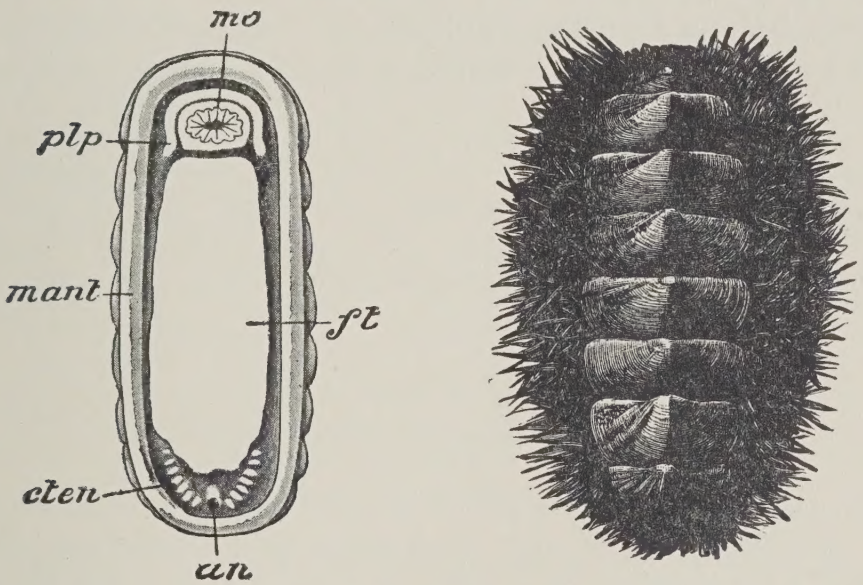

FIG. 95—THE CHITON

Right, from above; left, from below. *mo*—mouth; *mant*—edge of mantle; *ft*—foot; *cten*—gill; *an*—anus.

—or as we now say, adopting Haeckel's term for the superclass, "phyla"—groups which persist wholly, or with some modifications to be mentioned, in the classifications adopted by present-day zoologists. The segmented worms (*Annelides*) were removed from their association with Arthropods under Cuvier's Articulata by von Subold, who, in 1845, introduced the term Arthropoda. The second of Cuvier's two divisions is foreshadowed in Lamarck's scheme—though Lamarck excludes the clams—and

it is, therefore, fitting to pause at this point and examine the character of the Molluscan phylum as illustrative of the Principle of Unity of Type. The group to-day by general agreement includes two of the Cuvierian classes whose names appeared in Lamarck's scheme (Cephalopoda and Gastropoda), the former including squids, octopus, etc., the latter snails, limpets, slugs. In addition it includes Lamarck's separate class "Conchifera," since usually called Lamellibranchiata (the term used in Owen's lectures, 1855) or Pelecypoda by some contemporary authors. These were included along with the Tunicata that are now regarded as allied to Vertebrates in Cuvier's term Acephala. Cuvier's

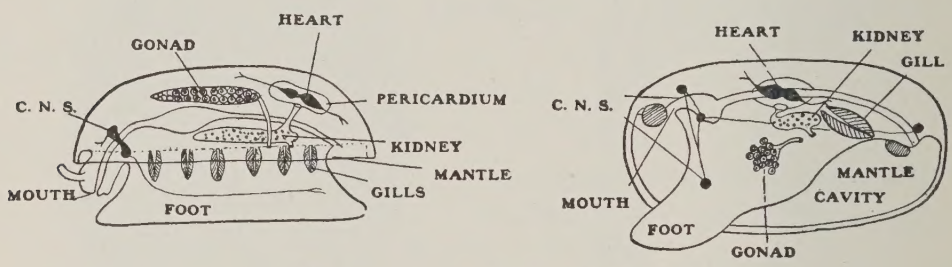

FIG. 96—UNITY OF TYPE IN MOLLUSCA

Comparison of anatomy of chiton and a bivalve.

Pteropoda are now regarded as an order of Gastropods. Of the Brachiopoda and Cirrhopoda (Cirripedia) we shall speak later. They have only the most superficial resemblances to the three major classes of Mollusca (Cephalopoda, Gastropoda and Lamellibranchiata). When we compare it with Linnæus' order of the same name, an assemblage which took in sea-anemones, sea-cucumbers, jellyfishes, most free living worms, we see that Cuvier's Mollusca, as far as the detailed study of its constituent groups had progressed at the time, implies a definite recognition of the principle of Unity of Type. In the modern phylum Mollusca two classes have been separated from the older Gastropoda. These are the Isopleura, or chitons, and the Scaphopoda, or elephant-tusk-shells.

Molluscs, like Vertebrates, Arthropods and Annelids, have a gut with mouth and anus, a well-developed C.N.S. and a circulatory system. The group is a very compact assemblage on account of a large number of characteristics which are found in different classes, though it is difficult to define the phylum in terms of any single feature which is both diagnostic and universal. The central nervous system is mainly concentrated in a ring of ganglia around the mouth (as in Arthropods and Annelids). The heart with at least

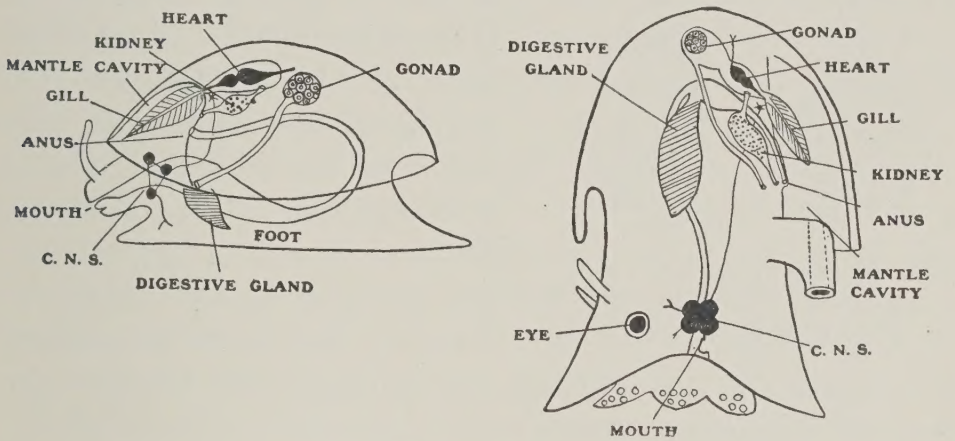

FIG. 97—UNITY OF TYPE IN MOLLUSCA
Comparison of a limpet and a cuttlefish.

two chambers lies in a body-cavity dorsal to the alimentary canal and communicates by a ciliated funnel with generally two (sometimes one) glandular organs, the so-called kidneys, which also communicate with the exterior. Typically the ventral aspect of the body is thick and muscular and constitutes a creeping foot. Typically also, there grows down from the side of the body a thin fold of integument known as the mantle, bounding a depression known as the mantle-cavity, in which are suspended one or more pairs of ctenidia or "gills." The ctenidium consists of a thicker axis with a series of thin plates on either side. Blood passes from the more muscular "ventricular" part of the heart by arteries to the tissues, thence to the gills, and from the gills by veins

returns directly to the thinner auricular portion of the heart. Thus the heart contains oxygenated blood and not de-oxygenated blood as in fishes. A characteristic, though not universal, feature of the group is the presence of a tongue (odontophore) bearing a thin ribbon of chitinous teeth known as the radula. Another characteristic feature of the group is the ciliated larva with its minute shell. It is called the Veliger (Fig. 98), and is sometimes preceded by a larval form which resembles the larva of marine worms, and is known as the Trochophore (Fig. 98). The heavily yolked eggs of the Cephalopods do not hatch out as larvæ. The unity of the Mollusca can be best appreciated by studying first the chiton (Figs. 95, 96), a common sea-shore mollusc, as the most generalised representative. The five classes into which the Mollusca are now divided are as follows :—

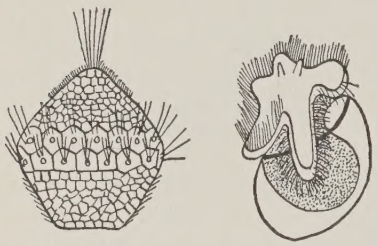

FIG. 98—CILIATED LARVÆ OF MOLLUSCS-TROCHOPHORE (left) AND VELIGER (right)

1. *Isopleura.*—The mantle-fold is co-extensive with the body, the mantle-cavity is shallow on either side carrying a paired series of ctenidia which hang freely. The foot is creeping and there is a distinct head, and odontophore and radula are present. A series of unpaired dorsal plates form the shell, *e.g.*, Chiton.

2. *Pelecypoda.*—As in Chiton the mantle-fold is co-extensive with the body, but is much deeper, so that the mantle-cavity is wrapped round the foot. The two lobes of the mantle-fold secrete a bivalved shell. The head, odontophore and radula are completely absent. A pair of ctenidia are present, the axis being fused along its whole length with the mantle-ridge, and the filaments, which are very numerous, hang downwards like a double curtain into the mantle-cavity. It is to this feature that the

alternative name Lamellibranchiata refers. The gill of a typical clam is not obviously like that of other molluscs, but a series of forms connect the more specialised type of gill, which we have described in the case of the mussel (p. 36), characteristic of the majority of the group, with the more typical Molluscan ctenidium of the smaller clams like Nucula. To this class belong the oysters, mussels, cockles, etc.

3. *Scaphopoda.*—The Scaphopods in general plan of organisation are very much like the Lamellibranchs, but the folds of the mantle-cavity fuse below the foot and secrete a continuous cylindrical shell. The ctenidia have been lost. There is a vestigial head and odontophore but no radula, *e.g.*, Dentalium.

4. *Gastropoda.*—These possess a well-developed head bearing tentacles and eyes and a creeping foot like that of Chiton, also an odontophore with radula. In early development the mantle-cavity is confined to the posterior region, but as development proceeds the visceral mass becomes twisted through two right angles so that eventually the mantle-cavity, anus, etc., are directed forwards. There is generally a spiral shell. In the primitive forms there are two ctenidia, more generally one, and in some forms, *e.g.*, snails and slugs, they have been lost. This class includes, in addition to the last-named, the whelks, limpets and sea slugs.

5. *Cephalopoda.*—The mantle-cavity is posterior and typically contains two ctenidia. The integument below the head is drawn out into elongated prehensile processes known as arms and also into a funnel-like opening for the mantle-cavity. There is nothing exactly like the creeping foot of Chiton. An odontophore and radula are present. The shell is single but is usually embedded in the dorsal wall, *e.g.*, octopus, cuttle-fish, squids, etc.

The Mollusca afford an important illustration of the unity of type within a group whose diagnostic features

cannot be summed up adequately by a few well-defined and entirely specific characteristics. Taking the snail, the oyster and the octopus as three molluscan types, the student may well be puzzled to see any such uniformity of structural peculiarities as we have encountered in the scorpion, the cockroach and the crayfish as examples of the Arthropoda. Yet the unity of the group is very clear, when we study a large number of forms. Thus the nautilus is clearly similar in its general organisation to the octopus, and the nautilus is not such a far cry from the whelk. The snail is clearly similar to the whelk, the whelk to the limpet, and the limpet in many respects resembles a clam, like Nucula, that has a typical molluscan ctenidium, though its resemblance to an oyster or mussel is not so obvious. Chiton occupies a central position with reference to all the classes of Molluscs. The zoological student who makes his first study in the field after a preliminary acquaintance with text book definitions may be disappointed to find that the exceptions at first sight seem to be as numerous as the rules. Later, as his knowledge increases, he realises that the diagnostic features usually assigned to a group are the most generally characteristic of innumerable points of resemblance, none of which are absolutely universal. To quote Darwin:—

> Nothing can be easier than to define a number of characters common to all birds; but with crustaceans any such definition has hitherto been found impossible. There are crustaceans at the opposite ends of the series which have hardly a character in common, yet the species at both ends, from being plainly allied to others and these to others and so onwards, can be recognised as unequivocally belonging to this and to no other class.

Progress of Comparative Anatomy in the Nineteenth Century. Actually the group Mollusca assumed its present dimensions as the seventh of Huxley's sub-kingdoms (1869) at a much later date than Cuvier's time. But it was Cuvier who made the first comprehensive dissections of

Molluscs, and his work really initiated a period of intensive comparative anatomical study no longer shackled by the medical pre-occupation with the Vertebrate body. These earliest dissections were not always very accurate in detail. It was in Germany that the most painstaking progress was made after Cuvier's death. One notices in the first comparative anatomists some attention to the rôle of the structures they described in the activity of the body—especially is this evident in the work of Milne Edwardes. In fact, the observers who established the Principle of Unity of Type were much less conspicuously pre-occupied with structure as an end in itself than were those of the Natural Selection period, which ensued in the second half of the nineteenth century.

Between the time of Cuvier and the middle of the nineteenth century anatomical study had developed along several different lines. A vastly greater number of animals from non-European countries had been secured for dissection. The study of the Vertebrate skeleton had progressed in relation to the rising importance of palæontology, or the investigation of fossil remains—especially under Owen. A new body of investigators into Vertebrate development under the leadership of von Baer, Remak and others, stimulated by the rise of the Cell doctrine, began to assert itself. Finally, with the rising importance of microscopic study, a great deal more information about marine organisms and their development was becoming available. In Marine Zoology two very notable contributions were made by an army surgeon, Vaughan Thompson, during the forties. These were, first, a recognition of the essential difference in organisation between the sea mats or *Polyzoa* and the hydroids; second, the description of the life history of the barnacles. Thompson's discovery that the sedentary stage of the barnacles is preceded by one in which the animal is a free-swimming crustacean (Fig. 94) relegated the class

Cirrhopoda or Cirripedia to an order of Crustacea and removed them from Cuvier's Mollusca.

This feature is incorporated in a classification published by the French zoologist, Henri Milne Edwardes, in 1855. The classification of Milne Edwardes, while retaining the four branches of Cuvier, shows the influence of the rise of embryology and the study of the Vertebrate skeleton, for in it the Mammals, Birds and Reptiles in the modern sense are grouped together, on account of the presence of fœtal membranes in development, as Allantoidians (Amniota of some later authors) in contradistinction to "Batrachia" and Fishes within the Vertebrate series. The Batrachia of Milne Edwardes appeared in Huxley's lectures (1869) under the more usual term, Amphibia. Thus the five great classes of Vertebrates assumed their present dimensions, and the only major change which has been made in these divisions is the separation from fishes of the lamprey and hagfishes as a class Cyclostomata on account of the absence of jaws and paired fins. This feature adopted by Haeckel (1868) is less important, as the Cyclostomes are essentially piscine in their circulatory and respiratory organs.

The classification given by Henri Milne Edwardes is as follows :—

FIRST BRANCH : OSTEOZOARIA OR VERTEBRATA

SUB-BRANCH 1. ALLANTOIDIANS

Class I. MAMMALIA

Orders : (*a*) Monodelphia : *Bimana, Quadrumana, Cheiroptera, Insectivora, Rodentia, Edentata, Carnivora, Amphibia, Pachydermata, Ruminantia, Cetacea ;* (*b*) Didelphia : *Marsupialia, Monotremata*

Class II. BIRDS

Orders : *Rapaces, Passeres, Scansores, Gallinæ, Grallæ, Palmipedes*

Class III. REPTILES

Orders : *Chelonia, Sauria, Ophidia*

Sub-Branch 2. Anallantoidians

Class I. Batrachians
Orders: *Anura, Urodela, Perennibranchia, Cœciliæ*

Class II. Fishes
Section 1. *Ossei*
Orders: *Acanthopterygii, Abdominales, Subbrachii, Apodes, Lophobranchii, Plectognathi*
Section 2. *Chondropterygii*
Orders: *Sturiones, Selachii, Cyclostomi*

SECOND BRANCH: ENTOMOZOA OR ANNULATA

Sub-Branch 1. Arthropoda

Class I. Insecta
Orders: *Coleoptera, Orthoptera, Neuroptera, Hymenoptera, Lepidoptera, Hemiptera, Diptera, Rhipiptera, Anopleura, Thysanura*

Class II. Myriapoda
Orders: *Chilognatha* and *Chilopoda*

Class III. Arachnida
Orders: *Pulmonaria* and *Trachearia*

Class IV. Crustacea
Section 1. *Podophthalmia*
Orders: *Decapoda* and *Stomapoda*
Section 2. *Edriophthalmi*
Orders: *Amphipoda, Lœmodipoda* and *Isopoda*
Section 3. *Branchipoda*
Ostracoda, Phyllopoda and *Trilobitæ*
Section 4. *Entomostraca*
Orders: *Copepoda, Cladocera, Siphonostoma, Lernœida, Cirripedia*
Section 5. *Xiphosura* [1]

Sub-Branch 2. Vermes

Class I. Annelida

Class II. Helminthes

[1] To-day an order of Arachnida: it includes the King Crabs.

Class III. Turbellaria

Class IV. Cestoidea

Class V. Rotatoria

THIRD BRANCH: MALACOZOARIA OR MOLLUSCA

Sub-Branch 1. Mollusca proper

Class I. Cephalopoda

Class II. Pteropoda

Class III. Gastropoda

Class IV. Acephala (=Pelecypoda or Lamellibranchiata)

Sub-Branch 2. Molluscoidea

Class I. Tunicata

Class II. Byrozoa

FOURTH BRANCH: ZOOPHYTES

Sub-Branch 1. Radiaria

Class I. Echinoderma

Class II. Acalepha

Class III. Corallaria or Polypi

Sub-Branch 2. Sarcodaria

Class I. Infusoria

Class II. Spongiaria

More detailed study of marine biology had already borne fruit in a new system which was propounded by Leuckhart (1848) in Germany. Leuckhart extends the principle of Unity of Type by breaking up Cuvier's Radiata into three groups, two of which persist almost entirely unchanged, except in the arrangement of the forms included therein, at the present day. These are the Cœlenterata and Echinodermata. Leuckhart also adopted the modern term Arthropoda, so that five of the dozen major phyletic groups which

are usually recognised to-day took shape about the middle of the nineteenth century. The remaining members of Cuvier's Radiata, now denuded of the Echinoderms and Cœlenterata, were placed by Leuckhart along with all worms in a new super-class (" Type " in his system) Vermes. The " Vermes " of Leuckhart and Haeckel was not a mere dustbin for animals about which little was known: its unity was definitely referred to what now seems to be a superficial resemblance of the ciliated larval forms which occur so often in the classes placed within that group. This we shall refer to later. Leuckhart's classification was as follows :—

TYPE 1: CŒLENTERATA

Class I. POLYPI
Orders: *Anthozoa* and *Cyclicozoa*

Class II. ACALEPHÆ
Orders: *Discophoræ* and *Ctenophoræ*

TYPE 2: ECHINODERMATA

Class I. PELMATOZOA
Orders: *Cistoidea* and *Crinoidea*

Class II. ACTINOZOA
Orders: *Echinida* and *Asterida*

Class III. SCYTODERMATA
Orders: *Holothuriæ* and *Sipunculida*

TYPE 3: VERMES

Class I. ANENTERÆTI
Orders: *Cestodes* and *Acanthocephali*

Class II. APODES
Orders: *Nemertini*, *Turbellarii*, *Trematodes* and *Hirudini*

Class III. CILIATI
Orders: *Bryozoa* and *Rotifera*

Class IV. ANNELIDES
Orders: *Nematodes*, *Lumbricini* and *Branchiati*

TYPE 4: ARTHROPODA

Class I. CRUSTACEA
Orders: *Entomostraca* and *Malacostraca*

Class II. INSECTA
Orders: *Myriapoda, Arachnida* (*Accra*, Latr.) *Hexapoda*

TYPE 5: MOLLUSCA

Class I. TUNICATA
Orders: *Ascidiæ* and *Salpæ*

Class II. ACEPHALA
Orders: *Lamellibranchiata* and *Brachiopoda*

Class III. GASTROPODA
Orders: *Heterobranchia, Dermatobranchia, Clepobranchia, Palmopoda* and *Cyclobranchia*

Class IV. CEPHALOPODA

TYPE 6: VERTEBRATA (Not specially dealt with)

Echinoderms and Cœlenterates. The Echinodermata, which include starfishes, sea urchins, feather stars, brittle stars and sea cucumbers, share one feature with the Cœlenterata. Both show a considerable measure—in some Cœlenterates complete—of radial as opposed to bilateral symmetry. In other respects they are very different.

Arthropods and Molluscs agree with Vertebrates in having a well-developed circulatory system. A rudimentary vascular system also exists in Annelids, Brachiopods, Nemertines and in Phoronis. The Echinodermata represent a definitely lower grade of physiological organisation and the classes, though differing in external form, have a close similarity in internal organisation (Fig. 99). A muscular integument with a leathery external covering and outer layer of ciliated epithelium is strengthened internally with calcareous plates

to which may be attached projecting spicules. It encloses a capacious body-cavity lined by secretory epithelium and developed as a pouch from the embryonic gut. The alimentary canal with mouth and anus runs through this body-cavity. From a certain number of grooves, typically five, on the external surface of the animal project a double row of hollow tentacles, each bearing a single sucker at its distal end. The cavities of these " tube feet " connect with a longitudinal vessel underlying each groove and discharging into a circular canal around the mouth. This canal communicates by a channel known as the stone-canal with the

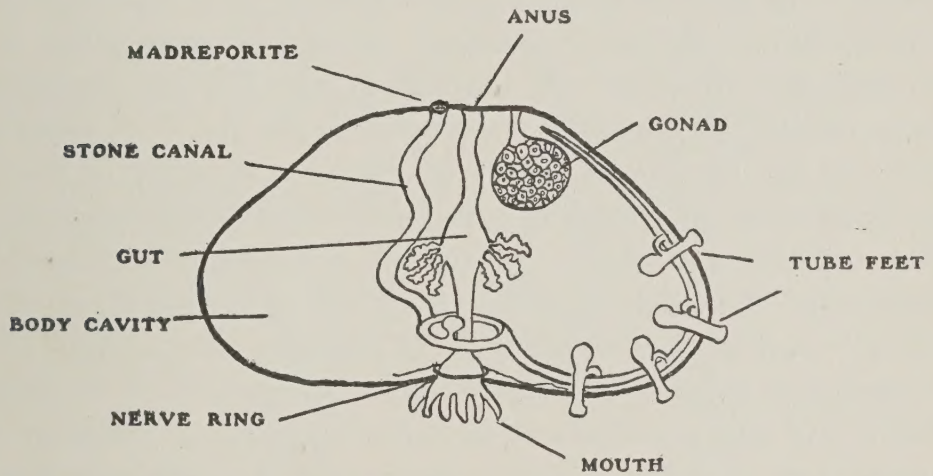

FIG. 99—DIAGRAMMATIC REPRESENTATION OF AN IDEAL ECHINODERM

exterior through a finely perforated plate, the madreporite. The gonads are arranged radially between the longitudinal canals of the tube-feet system, and communicate by short ducts directly with the exterior.

The group Echinodermata as defined by Leuckhart included one class which is represented by only a few species superficially not unlike the sea cucumbers. The " Sipunculoidea " are a very isolated group, to which reference will be made again; they have only the most superficial resemblance to any Echinoderm. With this exclusion, the existing forms are classified in five groups,

all of which, except the Ophiuroidea, appear in Leuckhart's scheme. These are :—

1. Echinoidea, *e.g.* sea urchins, heart and cake urchins, sand dollars
2. Asteroidea, *e.g.* starfishes
3. Ophiuroidea, *e.g.* brittle stars
4. Holothuroidea, *e.g.* sea cucumbers
5. Crinoidea, *e.g.* feather stars

The animals with which we have dealt so far are sufficiently large to be studied by gross dissection, which the earlier anatomists combined in many cases with experiment to discover the significance of the organs they described in the economy of the organism. With the recognition of the cellular structure of animals in the thirties embryology received an impetus : methods for the study of minute animals by the examination of microscopic sections were perfected, and new fields of comparative anatomy opened up. The microscopic study of tissues (histology) immensely facilitated the task of comparing the organisation of the simpler and more complex types of animals, but unhappily it meant less reliance on experimental evidence. It became more and more customary as time went on to think of a nerve, not as a tissue which propagates disturbances from one part of an organism to another, but as a tissue which, when treated with certain re-agents, stains in a particular way. The Cœlenterata afford an example of a group whose anatomical organisation could not be clearly appreciated until improved microscopic technique had been brought to bear upon it.

To attain a clear idea of the structural peculiarities of the Cœlenterata, a cursory study of the green Hydra (Figs. 100, 101) will assist us. This little organism which, when fully extended, may attain about half an inch in length, is found clinging to freshwater plants. It appears to the eye as a thread of bright green hue attached at one end to

some object and terminating in a tuft of delicate filaments (the tentacles) at the other. Sometimes it detaches itself and crawls by means of its tentacles which, when extended, may be twice as long as the rest of the body. When disturbed the whole animal, trunk and tentacles alike, shrinks into a swollen pear-shaped mass less than a fifth of its

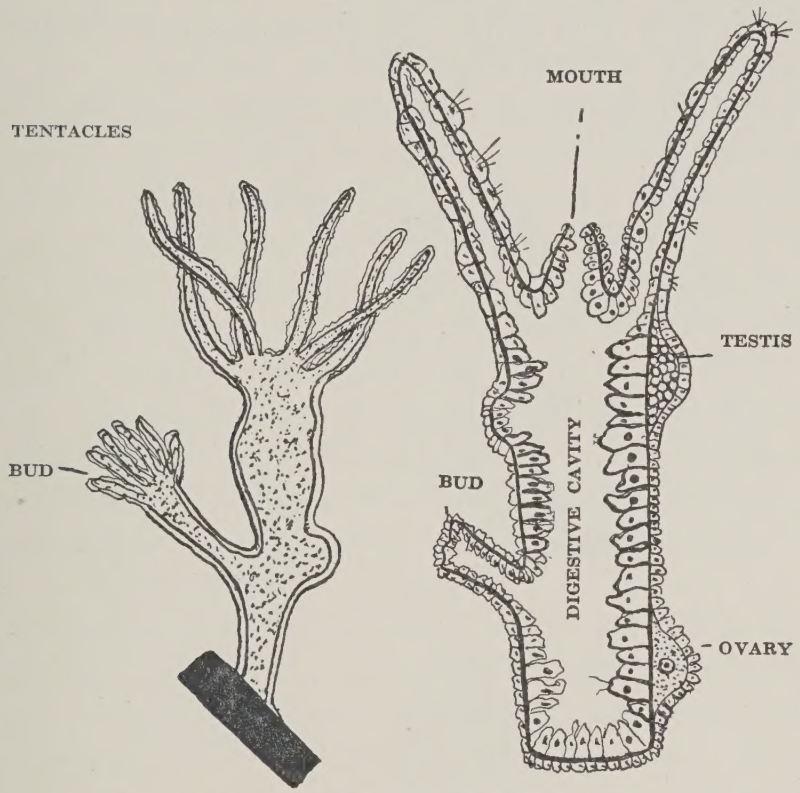

FIG. 100—THE GREEN HYDRA
Left, magnified about eight times; right, diagram of a vertical microscopic section.

extended length. It seizes small water fleas by its tentacles and engulfs them through a single aperture, the mouth, seen under the microscope to be situated at the tip of a small cone separated from the rest of the trunk by the crown of tentacles. When examined in thin sections, prepared by embedding the animal in wax, as is usually done with such small forms, the body is seen to be tubular. Its wall, consisting of two layers separated by a thin jelly, surrounds the cavity into which the food is thrust through the mouth.

The innermost layer consists of large cells, some of which are ciliated. The outermost portion of the body wall consists of several layers of smaller cells. Some of these are like ordinary epithelial cells in other respects, but their internal surface is drawn out into long contractile processes, on which account they are called epithelio-muscular or

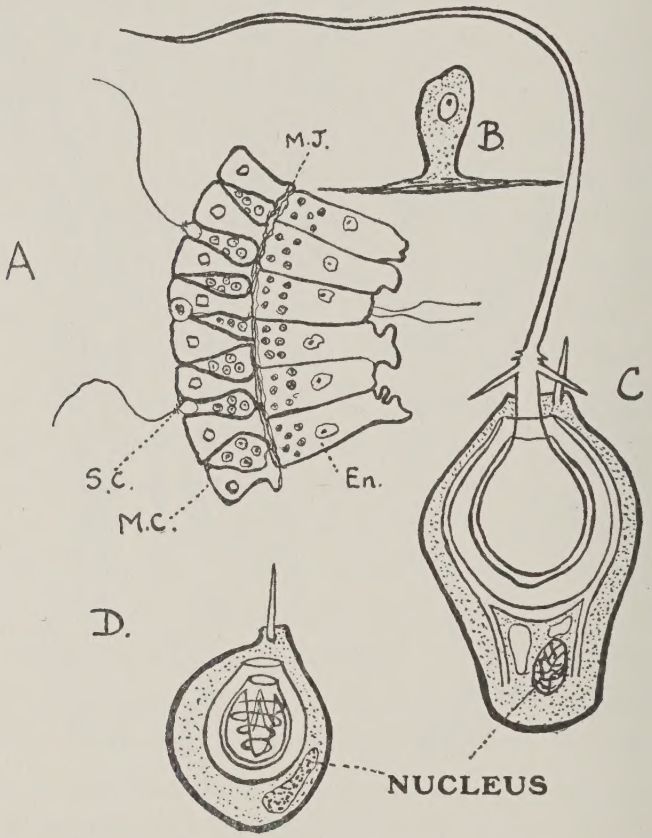

FIG. 101—HYDRA. MICROSCOPIC ANATOMY

A—Portion of body wall showing endoderm (En.), stinging cells (S.c.) and myo-epithelial cells (M.C.); B—Muscle (myo-epithelial) cell; C–D—Stinging cells (nematocysts).

myo-epithelial cells. Others especially abundant in the tentacles, and called stinging cells, contain ovoid vesicles like little flasks with the neck inverted. When the animal is disturbed these vesicles (nematocysts) thrust out their long filamentous necks, from the tip of which emerges a drop of a poisonous fluid. Between the epithelio-muscular

cells and the middle jelly there is a fine network of cells which stain like nerve tissue. This is called the nerve net, and experimental evidence shows that the Cœlenterate nerve net is a form of conducting tissue. From time to time cylindrical buds are formed on the sides of the trunk. These acquire a tuft of tentacles at the free end, and become detached to pursue an independent existence as new individuals. But in addition to this vegetative method of reproduction, true sexual reproduction occurs in Hydra. Cells of the outer layer of the body divide repeatedly, giving rise to sperms in the usual way, and the male gonad, which is seen as a prominence on any region of the trunk, is simply a mass of sperm covered by a thin pellicle of epithelial cells, which eventually becomes ruptured liberating the gametes. An ovary may be produced on the same individual. It consists of a single large ovum likewise covered by a thin epithelium on the outside of the body. The sperm penetrates through the ruptured wall of the ovary, and both fertilisation and early cleavage occur while the ovum is still attached to the body of the parent.

Budding occurs in many Cœlenterates and often the buds do not become detached, so that colonies are formed, as in such common rock pool Zoophytes as Obelia and Plumularia. In these colonial forms the sexual organs are often developed on a special sort of bud, the medusa, which is more flattened in shape than the hydroid. The medusa is set free into the water and pursues an independent existence for a time, shedding its sexual products when they are ripe. Many colonial Cœlenterates secrete calcareous deposits around them. Such are the corals. Some, allied to Hydra, form colonies with large floats filled with gaseous products, the zooids being clustered on the underside of the float which drifts with wind and current. Physalia, the Portuguese man-of-war, or blue-bottle, is one of these. In one respect the organisation of Hydra is simpler than that of the larger

Cœlenterata, the jellyfishes and sea anemones. It has no separate muscular system. Well-developed muscle fibres forming a continuous sheet in the outer portion of the body wall (jellyfishes) with, in addition, discrete bands in the inner portion (sea anemones) are often present in Cœlenterates. Again the gonads in the larger Cœlenterata are located in the digestive cavity. But in all cases they are simply proliferations of cells of the body wall, without any ducts or accessory structures. Stinging cells are always present, and the conducting tissue is of the diffuse type referred to as a nerve net. Separate afferent and efferent nerve fibres meeting in a central nervous system are never found.

The group Cœlenterata as defined by Leuckhart included the sponges, which are now usually made a separate phylum, the Porifera. With this restriction the Cœlenterata may be defined as follows. They are cellular animals with one cavity, the digestive cavity, communicating with the exterior by a single aperture, the mouth. The walls of the body consist of two series of cellular layers, the ectoderm and endoderm, separated by a gelatinous layer. In the cellular layers true muscle-fibres and conducting tissue may be differentiated, but there is never present either (*a*) a concentration of nervous elements to form a central nervous system or (*b*) a system of reproductive ducts. The germ cells are formed superficially either from the ectoderm (Hydrozoa) or endoderm. The main feature from a physiological point of view is the absence of a mechanism of true reflex action. The majority of Cœlenterates are thus divided by modern authors :—

1. *Hydrozoa.*—Gonads external, no gullet or gastric filaments, *e.g. Hydra, Plumularia, Obelia, Millepora, Physalia*

2. *Scyphozoa.*—Gonads internal, typically with alternation of generations, but the medusoid the predominant form. The medusoid differs from the Hydrazoan medusoid, in addition to

the internal gonads, in the presence of gastric filaments provided with stinging cells which are the remains of radial partitions in the hydroid from which they are budded off along the longitudinal axis, *e.g. Aurelia, Haliclystus* (sedentary), *Rhizostoma*

3. *Actinozoa.*—Gonads internal, but individuals entirely sessile with no alternation of generations. There is a deep ectodermal gullet and the digestive cavity is divided incompletely below the gullet and completely above by radial partitions which are provided with thick longitudinal muscle bands, *e.g.* sea anemones and the majority of the corals

A fourth group, the Ctenophora or comb-jellies, includes a few specialised forms with predominantly bilateral symmetry. In these the body muscles are laid down at an early stage in embryonic life, as in more complex animals.

The *Porifera* or sponges are only superficially like the Cœlenterata in so far as they represent a very low grade of physiological differentiation. They were regarded as animals by Aristotle, but they stand very much apart from all other animals, and such terms as body, individual, colony or the like have very little applicability to them. A sponge is a labyrinth of ciliated canals communicating by pores on the surface with the exterior. Between the canals is a gelatinous mass strengthened by horny fibres or spicules of calcareous or siliceous material, the exterior being invested in a thin epithelium in which distinct cell walls are absent. They have no nervous elements, and the reproductive organs are clusters of sperms or eggs embedded in the gelatinous coat.

We arrive then at this point: all the major phyletic divisions of animals were recognised by the middle of the nineteenth century with the exception of those groups which Leuckhart placed together in "Vermes." The main feature of systematic zoology in the second half of the nineteenth century was therefore the application of the Principle of Unity of Type to the sorting out of the constituent forms of this heterogeneous assemblage, but in addition a new

concept in classification came more prominently into play. This was the attempt to express in classificatory form the ancestral relationships implied in the evolutionary doctrine, and implicit in the systematic scheme of Lamarck. The influence of this new objective on zoological classification will be discussed later.

In a classificatory scheme put forward by Haeckel (1868) the same phyla (Haeckel's term) as those of Leuckhart were adopted, save for the textual difference that the Linnæan term "Zoophyta" replaced Cœlenterata, a practice in which Haeckel has not been followed by later writers. Haeckel's classes, however, correspond much more closely with those of more modern taxonomists. The Tunicata are removed from the Mollusca to "Vermes." And subsequent development has been mainly concerned with splitting up the latter into separate phyla, corresponding to its constituent classes in Haeckel's scheme. These are notably: Annelida, Nemathelminthes, Platyhelminthes, Rotifera (Rotatoria), Bryozoa (Polyozoa) and Tunicata.

The Segmented Worms. Let us first turn our attention to the *Annelida*, because they stand in a close relation to the Arthropoda, a relation expressed in Cuvier's Articulata and later in Huxley's Annulata, groups which are equivalent to the present Arthropoda with the addition of the Annelida.

The Annelida or segmented worms are externally segmented animals without limbs, but typically provided on either side in each segment with a tuft of bristles or setæ which serve for progression. The integument, which is covered externally with a thin layer of chitin, consists of an epidermis of one cell-layer together with an outer circular and inner longitudinal layer of muscles, and encloses a capacious cavity which is lined by secretory epithelium like the peritoneum of the Vertebrate. The alimentary canal runs from one end of the body to the other. The central nervous

system is of the same type as that of the Arthropod; a large pair of ganglia, situated dorsally in the pre-oral segment, connect on either side with a double chain of ganglia in

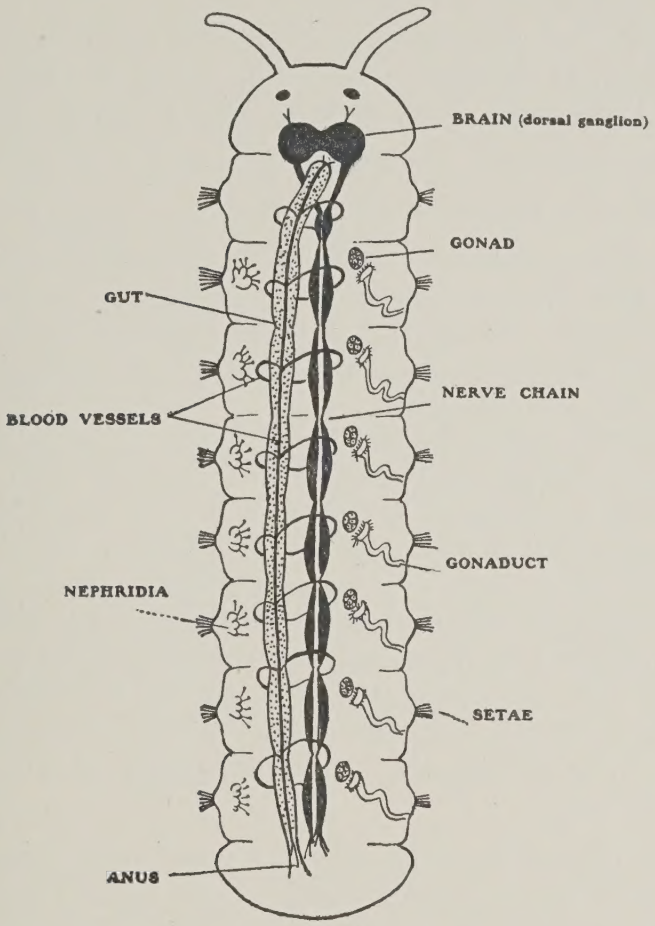

FIG. 102—DIAGRAMMATIC REPRESENTATION OF AN IDEAL POLYCHAETE

each segment more or less approximated ventrally beneath the alimentary canal (Fig. 102). The main trunks of the blood system are longitudinal vessels, typically containing hæmoglobin, running above and below the gut and connected by annular vessels in each segment. The gonads are present in several, sometimes in all, segments, in pairs, and discharge their products into the body cavity, whence they are conveyed by segmental ducts to the exterior. A paired

series of segmental tubules, the nephridia, thought to be of an excretory character, open to the exterior and end either blindly in flame-cells like those of flat-worms (*vide infra*) or by ciliated apertures into the body cavity. Annelids provide the most perfect examples of metameric segmentation, *i.e.* the repetition of structure along the main axis of the body, in the animal kingdom. So defined, the Annelida include the marine bristle worms, the earthworms and leeches, and these are customarily classified as follows :—

1. *Polychæta*—Marine worms with numerous setæ, usually projecting from cushion-like prominences on the side of the body, called parapodia. Often the pre-oral segment bears eyes and tentacles. The gonads are not localised, *e.g.* Nereis, Aphrodite, Arenicola, Bispira, Sabellaria.

2. *Oligochæta*—Earthworms and a few freshwater worms. Few bristles, no parapodia, eyes and tentacles never present. Hermaphrodite, gonads localised (*i.e.* restricted to certain segments) eggs laid in a cocoon, *e.g.* Lumbricus.

3. *Hirudinea*—Leeches. All semi-parasitic or blood-sucking. With few exceptions they have lost their setæ and the body cavity is largely replaced by connective tissue. They differ from the earthworms chiefly in possessing a sucker by which they adhere to their host or victim, and also in that each segment, corresponding to a nerve ganglion, etc., is externally divided into numerous rings, *e.g.* Hirudo.

To these classes must be added a number of minor groups (Echiuroidea, Myzostomida) which include very few animals.

The Annelida are sharply marked off from other " Vermes " by the segmental organisation and the well-developed body cavity. And it is for the former reason that they have often been associated with the Arthropoda. The fundamental similarity of the Arthropoda and Annelida is emphasised by the existence of the intermediate form Peripatus. The genus Peripatus, which is found in Africa, Malaya, South America and Australasia, has, like the worms, a continuous muscular tunic in its body wall and appendages, which are more like the parapodium of a Polychæte than the

walking legs of other Arthropods. But there is a fundamental difference between the Arthropoda and the worms in the character of the blood system, which is a closed circuit of vessels in the Annelida, whereas in Arthropoda—including Peripatus—an ostiate heart lies in a blood space which contains the internal organs. The merit of erecting a larger

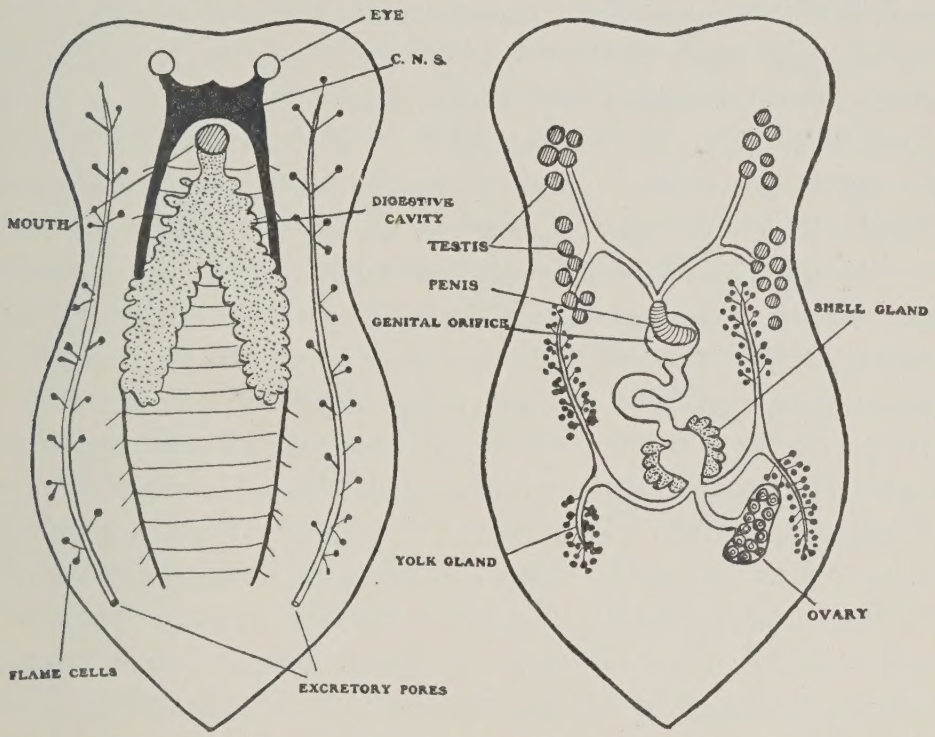

FIG. 103—DIAGRAMMATIC REPRESENTATION OF AN IDEAL FLAT-WORM

Showing gut, nervous system and excretory organs on left, and reproductive organs on the right.

phylum to include the Arthropoda and Annelida, as was done by Cuvier and Huxley, is in fact closely analogous to the advantages (*vide infra*) of including the Vertebrates and certain other groups to be mentioned later in a larger phylum, the Chordata.

The Flat-worms. Like the Annelida, the *Platyhelminthes*, or flat worms, are well defined. This phylum is very largely composed of parasitic forms, the life histories of which have been worked out with some difficulty in comparatively recent

times. The Platyhelminthes like the Cœlenterates have one principal cavity, the digestive cavity communicating with the exterior by a single aperture, the mouth. They have, however, no sign of radial symmetry, and a somewhat elaborate system of generative organs discharge their products to the exterior by specialised gonaducts, provided with an elaborate system of glands which constitute the most characteristic feature of the group (Fig. 103). The reproductive organs are with one or two exceptions hermaphrodite. The oviduct generally receives the secretion of shell glands and a ramifying system of yolk glands which occupy a good deal of the internal space of the body. Between the muscular outer wall and the epithelium of the gut the interspaces are filled with a highly characteristic mass of vacuolated cells called parenchyma. There is a ramifying system of intracellular tubules called the nephridia, communicating at one end with the exterior and ending at the other end blindly in cells with vibratile cilia which project into the lumen of the tube. They are called flame cells. In general all the Platyhelminthes are dorso-ventrally compressed. A central nervous system is present and consists of a large anterior dorsal ganglion and lateral cords connected by transverse commissures below the gut. Three classes are now recognised within the group :—

1. *Turbellaria.* Free-living flat-worms in which the body is covered by a ciliated epithelium, some of the cells of which contain hyaline bodies known as rhabdites. The mouth is typically at the end of an eversible pharynx on the ventral side. They are found under rocks in fresh and marine water. A few live in mud, *e.g. Planocera, Planaria, Bipalium.*

2. *Trematoda.* Parasitic flat-worms (flukes) in which the external epithelium after secreting a thick cuticle degenerates. The body is provided with suckers. A gut is present, *e.g. Distomum, Polystomum, Bilharzia.*

3. *Cestoda.* The integument and reproductive organs are very similar to the Trematoda, but a digestive cavity is absent. They are all internal parasites (tape-worms), and generally the

body is divided into a number of segments, each with a complete set of reproductive organs, *e.g. Tænia.*

The class *Nemertinea* in several respects show a considerable advance in structural complexity upon the flat-worms, for which reason they are properly elevated by most writers to phyletic rank. The elongated vermiform body with terminal mouth and anus and a rudimentary circulatory system at once separates them from the foregoing classes, as does the peculiar eversible pharynx enclosed in a tubular sheath above the alimentary canal at the anterior end of the body. On the other hand, a clear relationship to the Turbellaria is seen in the ciliated epidermis, the cells of which contain rhabdites, in the parenchymatous tissue that occupies the space between the gut and the integument, in the nephridia and nervous system. The Nemertinea occupy a very interesting position in the animal kingdom, in some respects intermediate between the Annelida and the Flat-worms, and they might well be conceived to be survivors of a group very closely related to the common stock of Annelids, Molluscs and Arthropods.

Thread-worms. Another group which includes forms of economic importance is the Nemathelminthes or round-worms, which comprises both a large number of parasites, chiefly intestinal, and free living forms in sea water and damp soil. The majority of forms denoted by this term are included in a class, Nematoda, or thread-worms, and it is doubtful whether the other classes usually associated with them have any close resemblance (Nematomorpha, which occur as parasites in the intestines of insects, and Acanthocephala, gutless intestinal parasites in Vertebrates, with a hooked eversible proboscis). The Nematodes have an elongated body covered with a thin cuticle with terminal mouth and anus at the opposite extremity. There is a muscular pharynx, but the rest of the straight alimentary canal is composed only of epithelium surrounded by cuticle. Between

the integument and the gut is a capacious cavity in which the gonads and coiled gonaducts lie. The cavity is not lined by a secretory epithelium like the body cavity of an Annelid. The integument itself consists of an epithelium below the cuticle and a single layer of longitudinal muscles with peculiar protoplasmic processes projecting freely into the body cavity. The similarity between the body cavity (or cœlom) of segmented worms, Vertebrates and Molluscs was a topic for much discussion and endless speculation during the second half of the nineteenth century. The fact that the "cœlom" arises in development in a different manner within the same group makes such discussion somewhat barren. To the Nematoda belong the horse thread-worm Ascaris (Chapter VI), the miner's worm Anchylostomum, and other human parasites such as Trichina, Filaria, and Oxyuris, the pin worm of children's stools. The remaining Vermes are isolated groups of little practical significance.

The *Rotifera* may be mentioned first, because they have always proved a source of attraction to amateur microscopists, and have for that reason been studied more thoroughly than most of the others. The Rotifera are minute animals found in fresh water the world over and occupy a very isolated position in the animal kingdom. Though of microscopic dimensions—the largest are only just visible to the naked eye—they have a comparatively complex organisation. The body is of various shapes and typically there is a circle of ciliated cells at the oral end. The alimentary canal is provided with mouth and anus and a gastric mill, but has no muscular wall. It lies in a capacious cavity in which nephridia with flame cells and gonads and gonaducts are also present. Both the latter open into the hind end of the gut. The C.N.S. is a circumœsphageal ring with a large bi-lobed dorsal ganglion. They are of no economic importance. Many are parthenogenetic, and like the social Hymenoptera, produce their males by virgin birth and their females from fertilised eggs. Some, like the gall-flies, and a few fresh-water Crustacea, have a regular alternation of parthenogenetic and bi-sexual generations. The Rotifera attracted a good deal of attention at one time

because of their—perhaps—superficial resemblance to the ciliated larvæ of Annelids, Molluscs and Flat-worms.

The *Polyzoa* are colonial animals, which in the form of the colony and the zooids show a superficial resemblance to corals and hydroids, from which they were first separated by Vaughan Thompson. There is a circlet of tentacles round the oral end leading into the alimentary canal which is provided with an anus and surrounded by a body cavity in which the gonads lie. The C.N.S. is represented by a small ganglion between mouth and anus. There is a ciliated larva somewhat like the trochophore larva of Annelids. Representatives of the group are common in rock-pools between tide marks. The Polyzoa are of very

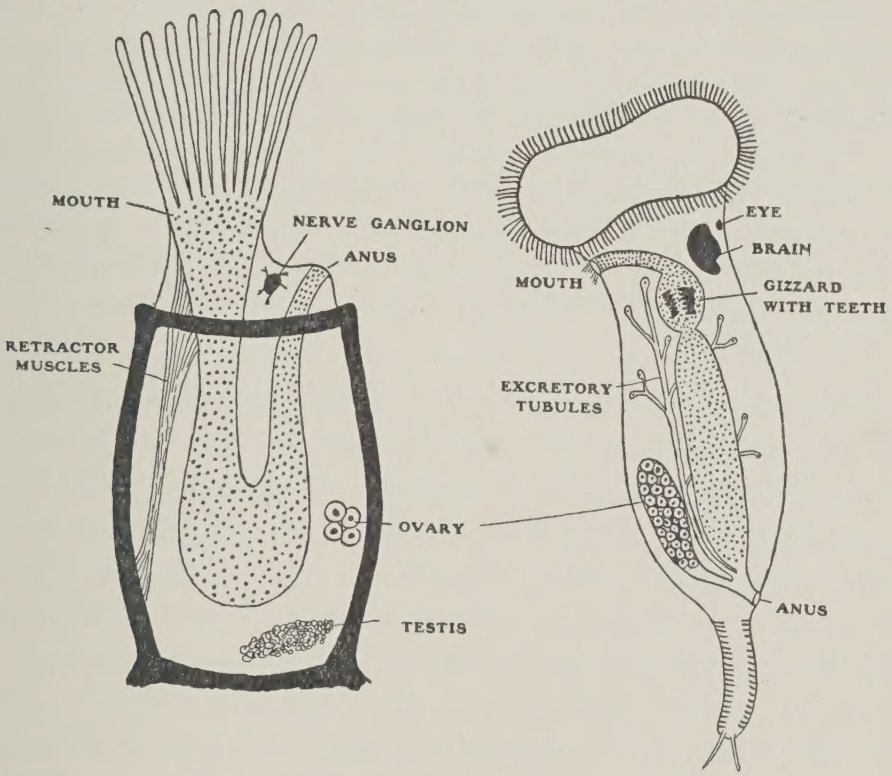

FIG. 104—DIAGRAMMATIC REPRESENTATION OF A POLYZOA (left) AND A ROTIFER (right)

uncertain affinities. Some authors, following Huxley, associate them with the lamp-shells or Brachiopoda which superficially resemble bivalve molluscs. Others merge both groups along with the classes Phoronidea and Sipunculoidea and certain other forms in a Phylum Podaxonia, or Molluscoidea.

The *Sipunculoidea* are vermiform organisms suggestive of Annelids. They differ, however, from the Annelida in the total absence of segmentation or setæ and the position of the anus, which is dorsal and near the anterior end. Sipunculoids may be recognised by their ability to introvert the anterior extremity of the body. They are common on beaches but live inconspicuously in crevices in rocks, or burrowing in sand or mud. The body cavity contains corpuscles coloured by a red respiratory pigment, oxyhæmerythrin, which in the reduced form is colourless. The Sipunculoidea along with the Echiuroidea, now transferred to the Annelida, were placed in Haeckel's classification in a class, Gephyrea. The process of splitting up the "Vermes" into assemblages of forms based on Unity of Type is not as yet completed, that is to say, it is not one on which unanimity has been reached. If we exclude the Tunicata—about which more must be said later—the following represent a by no means exhaustive list of separate phyla recognised by modern authors under Haeckel's Vermes: Annelida, Platyhelminthes, Nemertinea, Nemathelminthes, Rotifera, Brachiopoda, Polyzoa, Sipunculoidea, Phoronidea, Priapuloidea, Chætognatha. But some of these terms (*e.g.* Polyzoa) may include forms which should be further separated.

Allies of the Vertebrates. One class included in Haeckel's Vermes is a group which has had an erratic history in zoological classification, and like the barnacles, one whose present position in the animal kingdom is based more on its larval than upon its adult characteristics. The Tunicata or sea-squirts were placed at one time among the Molluscs. This association has no justification in the light of what we know of either their adult or larval characters. Their present position in zoological classification, like that of the barnacles, illustrates the extension of the Principle of Unity of Type to the study of all stages in the development of an animal.

In Flat-worms, Nemathelminthes, Annelids, Molluscs and Arthropods, there is one underlying feature of similarity in the general architecture of the body, especially in relation to the relative positions of the C.N.S. and gut, namely,

the presence of a dorsal ganglion above the mouth and a pair of lateral nerve-cords, which tend to be approximated ventrally below the gut, forming a circumœsphageal ring in all except the flat-worms. In the Vertebrate phylum the C.N.S. is wholly dorsal to the gut and arises as a median tubular infolding of the ectoderm or outer skin of the embryo. This feature of organisation together with certain minor points is shared by a few other forms. For this reason many authors have relegated the Vertebrata (or Craniata) to a sub-phylum of the phylum *Chordata*, which is distinguished by the above characteristics, and the presence of pharyngeal clefts and a notochord at some stages of development. It is within this assemblage that the Tunicata are placed.

The Vertebrates, however, form such a compact group, so sharply distinguished in particular by (1) the head with its characteristic sense organs, eye muscles and cranial nerves (2) the circulatory system, that this procedure does not seem more justifiable than placing the Arthropods and Annelids in one phylum. The groups that have been added for the construction of the phylum Chordata are :— (1) the Cephalochorda ; (2) the Urochorda or Tunicata ; (3) the Hemichorda. Of these the first two are undoubtedly closely related to the stock from which Vertebrates arose. The affinities of the third are not so convincing. To avoid multiplication of phyla we shall consider these three groups under the phyletic heading *Prochordata*.

1. *Cephalochorda.* The Cephalochorda are, of all the Prochordata, most like Vertebrates, and are represented by a single marine genus Amphioxus, whose distribution is world-wide. It was placed by Pallas (1788) in the Linnæan genus Limax among the slugs as Limax lanceolatus. It was lost to the zoological world again till 1834, when Costa renamed it Branchiostoma and recognised its affinities with the Fishes. Two years later Terrell (1836) redescribed it

under its present name in *The History of British Fishes.* It appears as the sole representative of an order of fishes in Huxley's classification (Pharyngobranchii) and as a separate class of Vertebrates in Haeckel's *Leptocardii.* In fact it is as distinct from the true Vertebrates or Craniata as are the sea-squirts. It is a fish-like form, burrowing in sand, and having a decided and not wholly superficial resemblance to the larval form of the lamprey. The myotomes or muscle segments are like those of a fish, save that the segmentation extends to the anterior extremity. The spinal nerves have dorsal and ventral roots which do not unite. The Vertebrate sense organs, eye muscles, etc., are absent. The circulatory system without heart or red blood corpuscles is very poorly developed. The notochord extends to the anterior extremity and is co-extensive with the whole length of the body. One peculiar feature of Amphioxus is the presence in the dorsal part of the body cavity in the pharyngeal region of a paired series of nephridia with flame cells, extraordinarily like those of Polychætes. The gut is straight and perforated for about half its length by fine pores, so that in this region of the pharynx its walls are like a sieve. The pores do not lead directly to the exterior but into a cavity—the atrium—formed in development by the downgrowth of two flaps of the body wall which meet ventrally so as to constitute a closed chamber which communicates with the exterior by a mid-ventral aperture behind the pharyngeal region. The entire internal wall of the pharynx and sides of the pores are lined with ciliated epithelium, and the cilia are so arranged as to constitute a food-net very much like the gill of a clam in its operation. The lateral cilia which line the pores create a current from the mouth into the atrium. From a ventral groove or endostyle a sheet of mucus is thrown on to the sides of the pharynx by longitudinal rows of long cilia. The facial cilia which line the internal walls of the pharynx wash this

sheet of slime with entangled food particles up to a dorsal groove whose cilia maintain a current backwards towards the intestine. An endostyle like that of Amphioxus is present in the lamprey larva. It becomes separated off at metamorphosis to form the thyroid gland.

2. *Urochorda* (*Tunicata*). The Urochorda or Tunicata (Fig. 105) are a more comprehensive group than the foregoing. Their association with Amphioxus dates from the researches of the Russian zoologist Kowalewsky (1866), who first elucidated the life history of the sea-squirts and of Amphioxus. They all agree in having a dorsal tubular C.N.S. at least at one stage in development, and an elongated well-defined notochord restricted to the tail region of the body which is of tadpole-like configuration in the larval stage. The characteristic Vertebrate sense organs are lacking in the tadpole larva, but the anterior end of the C.N.S. is enlarged to form a brain. In one group of Tunicates (Larvacea) the tadpole-like form of the body with its notochord and dorsal nerve is retained throughout life. In the largest group (Ascidiacea) the larva attaches itself at the time of metamorphosis to some surface by the head region (cf., the barnacles); the tail and notochord are absorbed; and the C.N.S. persists as a ganglion between the mouth and anus, which has shifted through 180°. The whole body is enveloped in a thick cellulose case or test. The only trace of chordate characteristics that the adult retains is the sieve-like pharynx surrounded by an atrial cavity. This structure with its endostyle is remarkably like that of Amphioxus, constituting a ciliary feeding mechanism. Some forms are solitary, others by budding give rise to colonies of individuals embedded in a common test and sometimes connected with one another by a stolon. The beautiful luminescent Pyrosoma forms cylindrical pelagic colonies. In a third group (Thaliacea), including two pelagic forms, Salpa and Doliolum, which are widely

distributed, the adult form is essentially very much like a simple Ascidian, but it is not sedentary. These forms have a regular alternation of sexual and asexual generations, the sexual individuals being formed as small buds from a ventral appendage known as the stolon. Both simple and colonial Ascidians are common between tide-marks on rocky shores. The simple Ascidians (sea-squirts, red-bait, etc.) are unmistakeable objects. The colonial Ascidians are easily mistaken for sponges.

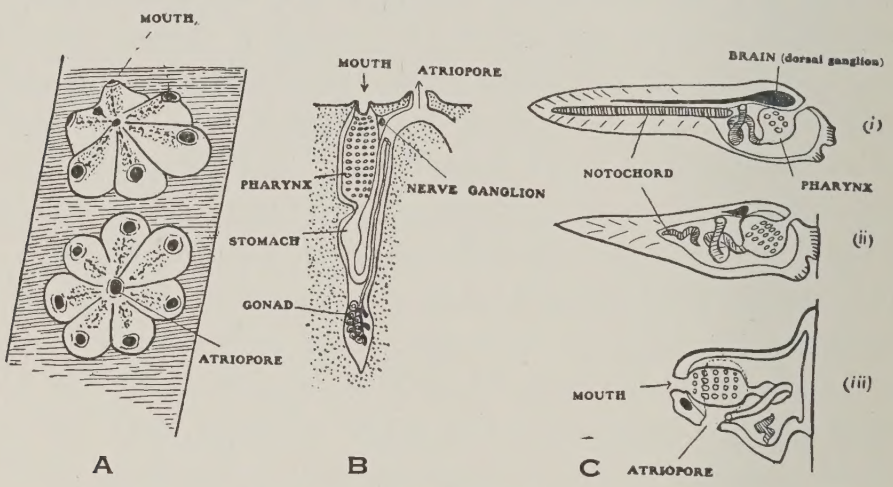

FIG. 105—TUNICATA

A—Colonies of a sea-squirt attached to a piece of weed; B—Longitudinal section through single zooid of a colony; C—(i) The tadpole-like larva undergoing metamorphosis (ii)–(iii).

3. *Hemichorda.* The Hemichorda are of much more doubtful position than the foregoing and include two groups. The Enteropneusta are typified by the burrowing marine acorn-worm, Balanoglossus. The acorn-worms, distinguished by the conical proboscis in front of the mouth, followed by a thickening of the integument known as the collar, are placed near Amphioxus and the Tunicates, chiefly on account of the structure of the pharynx, which is perforated in a manner extraordinarily similar to that of Amphioxus. It communicates with an atrial cavity that is, however, dorsally and not ventrally placed. A diverti-

culum from the gut extending into the proboscis region has been compared to the notochord. The C.N.S. is represented by dorsal and ventral cords lying immediately under the epidermis. The acorn-worms have a free-swimming ciliated larva which strikingly resembles that of the sea-cucumbers. Placed near the Enteropneusta is a group of colonial organisms (Pterobranchia) superficially resembling Polyzoa. The zooids have the body divided into a proboscis, collar and trunk like the acorn worms. These have pharyngeal clefts and a structure resembling the supposed notochord of Balanoglossus. From the collar region a ring of fine tentacles protrudes. The chordate characteristics of the Hemichorda were first emphasised by Bateson (1884-6), whose views have been very widely but not universally accepted by systematic zoologists.

The Outcome of Comparative Anatomy. What, we may ask, was the positive outcome of the advances in the study of comparative anatomy during the first three quarters of the nineteenth century? We started with the recognition that the majority of animals fall into well defined groups distinguished by a variety of structural peculiarities affecting their entire organisation, peculiarities that have no conceivable utilitarian significance. The task of sorting out animals of different kinds into such groups, though a purely descriptive one, played a tremendous part in creating a new mental attitude to the diversity of animal life. The once popular standpoint which saw in every similarity and difference the evidence of special design became more and more barren. But that was not all. As zoology progressed under the influence of the Principle of Unity of Type it became more and more evident that, while the vast majority of animals alive to-day fall into clearly defined assemblages, we constantly encounter isolated forms which bridge over the big gaps in our classificatory schemes. Such forms are Peripatus,

Amphioxus and the Nemertinea for instance. Thus when, after the formulation of the Principle of Succession, which we shall next discuss, evolutionary speculation revived, it seemed only natural to regard these intermediate forms as survivors of older stocks; and biologists now began to construct hypothetical pedigrees embodying the idea of ancestral relationship in their classificatory schemes. The net result of the researches which progressed under this new stimulus was to show that an evolutionary interpretation of the diversity of animal life is perfectly consistent with the facts as we know them. This was a necessary phase in the development of the evolutionary theory, but we can see, looking backwards a little, that a generation of biologists became more and more divorced from the experimental study of activity to which the earlier naturalists like Milne Edwardes were by no means indifferent, and this generation became at the same time less and less disposed to put to the test of experimental demonstration the fundamental postulates of the Evolutionary Hypothesis.

Chapter XI [1]

THE PRINCIPLE OF SUCCESSION IN SPACE AND TIME

WE have now to turn to the third of the great historical steps in the building up of the Evolutionary Hypothesis enumerated in a previous chapter. It is the masterly way in which Darwin marshalled the facts at his disposal in presenting this aspect of the case that constitutes his chief claim to have made an enduring contribution to the Evolutionary Theory. From ancient times, but more especially from the end of the seventeenth century onwards, the hard remains of animals were unearthed from time to time—shells, for instance, of molluscs which only live in water were found far inland remote from lake, river or sea. But such relics were attributed by the current mythology of Christian countries to the deluge that destroyed the contemporaries of the Noah family; and sceptics like Voltaire, who ventured to offer more naturalistic hypotheses, were hardly more happy in their speculations. An exception must be made in favour of Xenophanes (B.C. circa 500), and independently the Arab physician Avicenna, who recognised fossils, it appears, as remains of animals formerly alive, and saw in them evidence of the existence of oceans where there is now only land. A giant fossil salamander

[1] The subject matter of this Chapter should be supplemented by a comparative study of the skeletons of the frog, man, the fowl, the crocodile or tortoise, and the dogfish in the laboratory; demonstrations of the scaly armour of the sturgeon or bony pike, and visits to a museum where specimens of fossil Vertebrates are exhibited.

which occurs abundantly in the Upper Miocene of Switzerland, closely related to the Japanese salamander Cryptobranchus japonicus, was unearthed by Scheuchzer in 1726, and named *Homo diluvii testis*. The motto attached to his figure reads :—

> Betrübtes Beingerüst von einem alten Sünder
> Erweiche Herz und Sinn der neuen Bosheitskinder.

Which is translated (*Camb. Nat. History*, viii., p. 84) :

> Oh, sad remains of bone, frame of poor Man of Sin,
> Soften the heart and mind of recent sinful kin.

Not less grotesque is the legend that attaches to the large fossil Foraminifer, Nummulites, which is found in limestones

FIG. 106—THE REMAINS OF A GIANT SALAMANDER UNEARTHED IN 1726 BY SCHEUCHZER OF ZURICH. IT IS DESCRIBED IN HIS MONOGRAPH AS "HOMO DILUVII TESTIS" (MAN ; WITNESS TO THE DELUGE)

across Europe and Northern Africa into India. According to Cole (*History of Protozoology*) the botanist Clusius (circa 1550) mentions that during the retreat of the Tartars before the Teuton soldiers coins were freely scattered as they fled with the object of diverting their pursuit. The manœuvre was not, however, successful, as the coins were

converted into stones, *i.e.* Nummulites, by the intervention of "an obliging and sympathetic Deity."

With the possible exceptions mentioned it seems that priority in the recognition of fossils as remains of what were once living animals is due to Steno (1699), a Danish anatomist who taught at Padua. It was, however, Cuvier's monograph on fossil remains that initiated the epoch of systematic palæontology. The effect of the researches of Cuvier's school was not felt till the Uniformitarian doctrine, *i.e.* the view that successive strata have been deposited by a continuous process, had been established, chiefly through the work of Lyell (1830). The impiety of this new Geology did not escape challenge. In the minutes of a meeting of the Geological Society of Great Britain in 1840, we read that the retiring president, Dr. Buckland,

> with a look and tone of triumph pronounced upon his opponents who dared to question the orthodoxy of the scratches and grooves of the glacial mountains the pains of eternal itch without the privilege of scratching.[1]

This doctrine lies outside the scope of our present studies; we shall have to assume the now universally accepted view that the various strata of which the earth's crust is composed have been laid down in orderly succession during periods of time compared with which that occupied by the history of human society is of negligible duration. Once this conclusion was accepted the study of fossils acquired a new interest and progressed rapidly under the leadership of men like Owen, Cope and their contemporaries. Students of fossils set themselves to compare the characteristics of animals in different geological epochs, and to elucidate evidences of a continuous succession of new forms of life handed down to posterity in the record of the rocks. Out of their studies the great Principle of Succession took shape.

[1] *Hist. of Geol. Soc. of Lond.*, p. 142.

Succession. The geological succession of organisms is demonstrated, first, by the fact that many of the more highly specialised and successful groups of the present day are not found to have existed at earlier periods of the earth's history, and were preceded by forms which are intermediate between them and representatives of surviving groups that were already existent before them; secondly, by the fact that the earliest members of the great groups are usually found to be of a more generalised type of structure than existing types. Adequate material for drawing these conclusions is provided only by forms which had resistant structures such as the Vertebrates, Arthropods and Vascular plants.

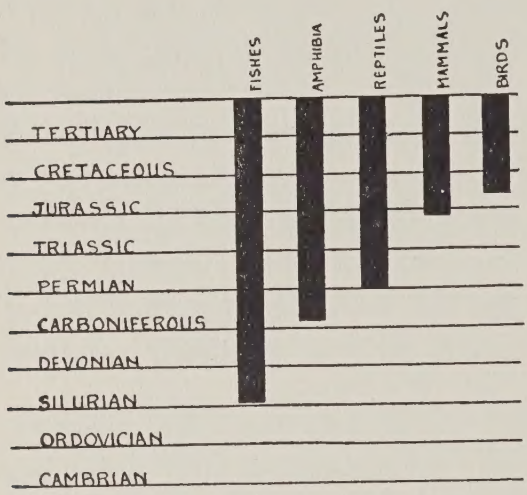

FIG. 107—THE SUCCESSION OF VERTEBRATES

We shall not in this chapter restrict ourselves to the evidence available in Darwin's time. Taking first the Vertebrates we find that the earliest remains of fishes appear in the Silurian (see Fig. 107). Amphibia appear in the earlier Carboniferous, Reptiles in the Permian, Mammals at the end of the Triassic, and Birds at the beginning of the Jurassic. The earliest group of modern fishes to become predominant were the most generalised modern group, the Cartilaginous fishes; and through the fossil "ganoids" of the late Silurian every stage in the evolution of the skull by the sinking in of bony scales in the head region can now be traced to the stage it had reached in the first land Vertebrates. Through the South African Triassic reptiles (Theromorpha) of the Karoo, an unbroken series of forms

link up the head, limb girdles and vertebral column of the Stegocephali to the more highly specialised structures of the mammals. The series linking the reptiles to the birds is less complete, but there are definite foreshadowings of the avian limb structures in the earlier Dinosaurs; and

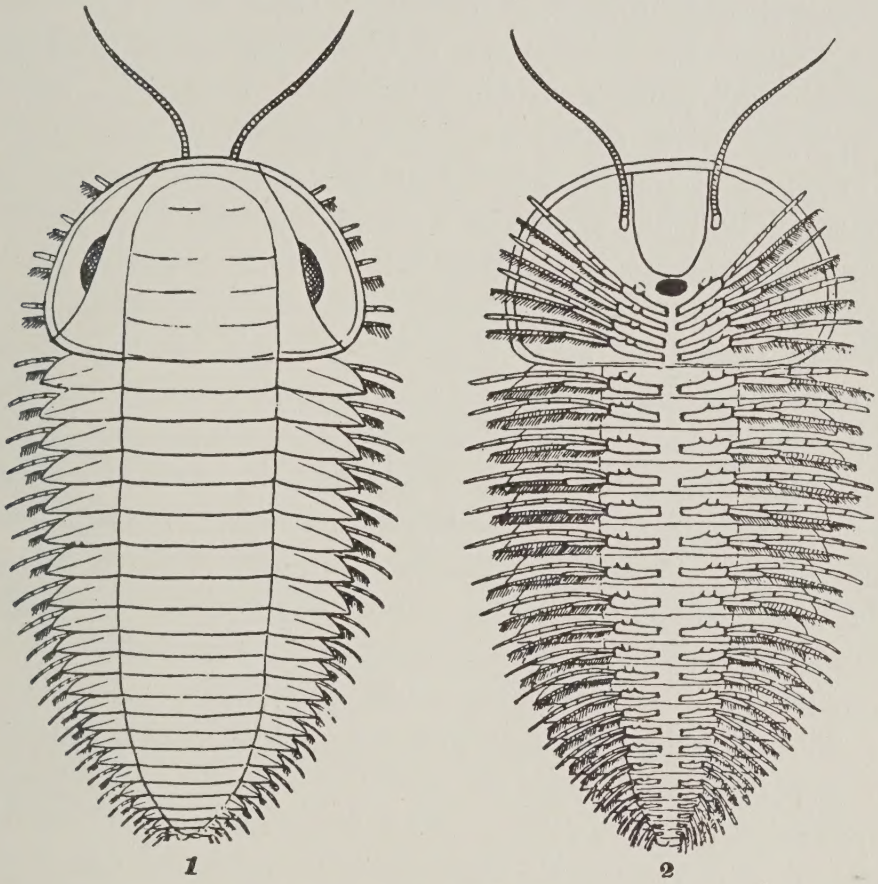

FIG. 108—A TRILOBITE
1—Upper surface; 2—Under surface.

the first undoubted bird, beautifully preserved in the Bavarian slate, has many striking reptilian features. The forelimb has three complete clawed digits with the normal number of phalanges. There was a long tail like that of a lizard. The skull had teeth and distinct sutures. A covering of feathers, however, leaves no doubt about the fact that Archæopteryx was essentially a bird.

In the Arthropod series, the earliest class to become dominant was the extinct Palæozoic and very generalised group, the *Trilobites*. Of modern groups, the Crustacea, which more than any other groups retain Trilobite features (*e.g.* biramous appendages), emerged in the Cambrian. Winged insects and land Arachnids like land Vertebrates first appear abundantly in the coal measures, and it is noteworthy that a more generalised group of aquatic Arachnids with some Trilobite features of organisation (Eurypterids) already existed early in the Palæozoic. The Trilobites were forms with a head bearing five pairs of appendages and a large number of trunk segments which were all alike. There was one pair of appendages in front of the mouth, and as in insects, Myriapods and Peripatus, this pair of appendages was antenniform. The trunk appendages were all two-branched or *biramous*, a condition found in the swimming appendages of practically all aquatic Crustacea to-day, and suggested by the form of the abdominal appendages in the Arachnid Limulus, and the legs of some wingless insects. All the trunk appendages had basal segments like the masticatory bases ("gnathites") seen in the anterior appendages of Arachnids. But, as in Arachnids, no pair of appendages is exclusively subordinated to masticatory activity as are the mandibles of insects, Myriapods and Crustacea. The Trilobites thus agree with Arachnids in having no mandibles, with insects and Myriapods in having one pair of feelers or antennæ, and with Crustacea in the biramous character of the trunk appendages (which were presumably for swimming). Thus there existed, as the predominant group of Arthropods at the time when the first representatives of any extant groups make their appearance, a class of forms which combine in their structure characteristics of all existing groups. Furthermore, the earliest Arachnids (*Eurypterida*) to become predominant are far more like the Trilobita than are many of the later and

FIG. 109—ARCHAEOPTERYX

now predominant representatives of the same class. It is therefore specially interesting that the preservation of the Trilobites is so perfect that we know as much about the external anatomy of several genera as we do about that of any extant representative of the Arthropod phylum. The King Crab, Limulus, is the sole surviving representative of an order of Arachnids closely allied to and contemporary with the Eurypterids. An aquatic scorpion Palæophonus, intermediate between modern scorpions and Eurypterids, occurred before the Carboniferous, though, as stated, typical land Arachnids first occur in the coal measures. In the Carboniferous, insects are abundant, whereas the Myriapods, which may be looked upon as intermediate in many respects between Trilobites and Insects, go back to the Cambrian rocks. The predominant group of insects in the Carboniferous was a winged order, the *Palæodictyoptera*, which are fairly well preserved, and are now totally extinct. These are very instructive, as indicating the existence of a series of forms intermediate between winged and wingless Arthropods ; for one genus, Stenodictya, in addition to having two pairs of fully-formed wings, carried small marginal wing-like projections on the first thoracic and eight of the abdominal segments.

Striking as is the evidence for a continuous succession of Arthropod types showing increasing divergence of structure, it is not so impressive as the survey of an immense body of data bearing on the history of the Vertebrate skeleton, more especially because quite highly specialised Crustacea were already emerging at the time when Trilobites were the dominant Arthropod group. In the case of Vertebrates on the other hand we have a phylum which does not appear to have been represented at all in the earliest fossil bearing rocks, while the majority of the classes of the phylum have come into existence since the time when the coal measures were laid down. The Principle of Suc-

cession can be traced through every aspect of the Vertebrate skeleton.

The History of the Vertebrate Skeleton. In what follows it will be assumed that the student will examine the main features of the skeleton in the laboratory or museum. The hard parts of Vertebrates include the following tissues—cartilage, bone, dentine and enamel. The first is a tissue which consists of cells more or less uniformly distributed in a gelatinous matrix. In this matrix calcium salts are often deposited, as in bone, but bone differs fundamentally from cartilage in that blood

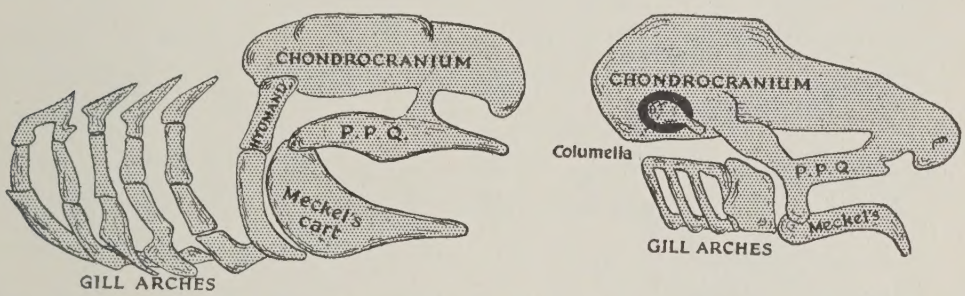

FIG. 110—CARTILAGINOUS SKULLS OF THE DOGFISH (left) AND THE FROG TADPOLE (right)

P.P.Q. is the quadrate or palato-pterygo quadrate bar.

vessels penetrate the matrix of the tissue and the cells are arranged concentrically around the canals in which the blood vessels lie. Enamel and dentine are respectively the outer and inner hard portions of our teeth.

At the end of the Silurian, fishes of two types make their appearance. One type is represented by forms which are most nearly like sharks among living forms, and may be classified among the *Chondrichthyes*, the group in which sharks, rays and dog-fishes are placed. In the Chondrichthyes the skeleton is entirely cartilaginous and the skull, like the embryonic cartilaginous skull of the later groups, consists of two distinct parts, the brain box or chondrocranium and the jaws. The upper jaw consists of a bar of

cartilage on either side, called the palato-pterygo-quadrate or more shortly the quadrate. The lower jaw consists of

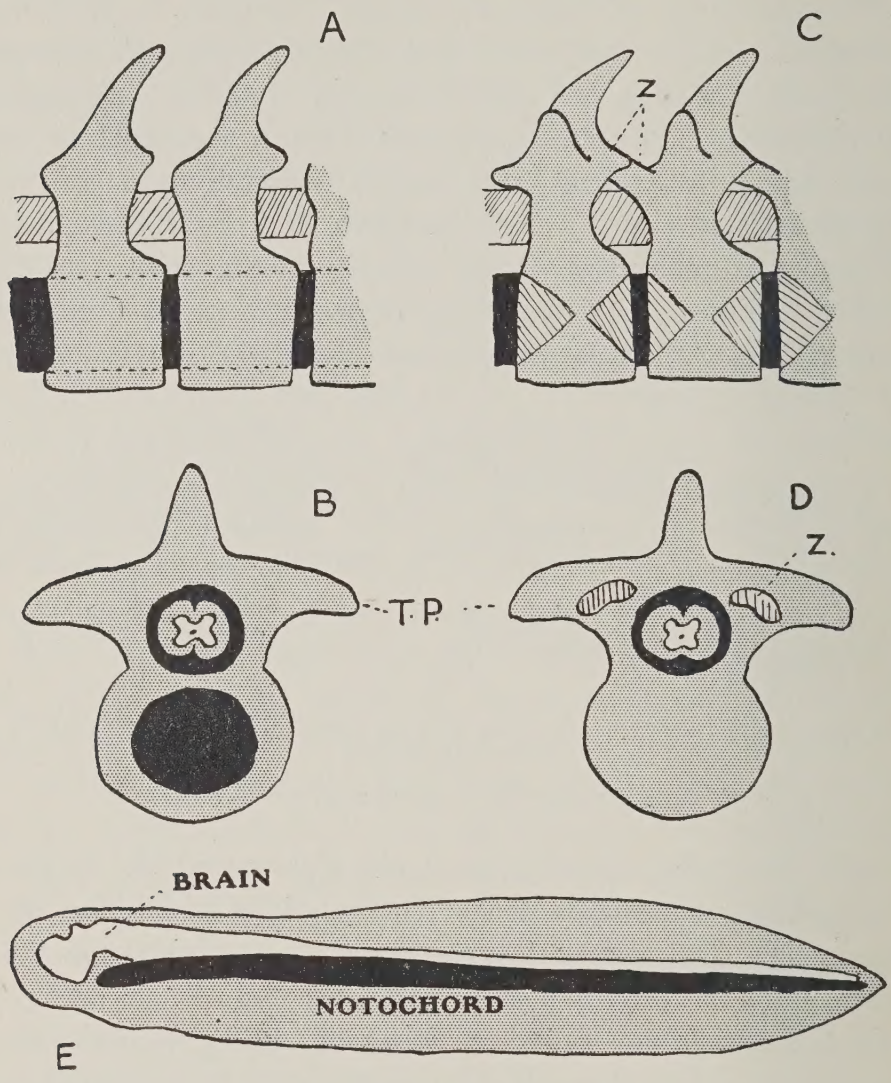

FIG. 111—THE AXIAL SKELETON

A B—Primitive vertebrae with persistent, unconstricted notochord and tubular vertebral centra; C D—Vertebrae with biconcave centra; Z—Zygapophyses or articular facets of the neural arches, the posterior zygapophyses of one vertebra overlap the anterior zygapophyses of the vertebra next behind; T.P.—Transverse processes; E—Vertebrate embryo showing notochord.

a bar of cartilage on each side, called Meckel's cartilage. The gill clefts in fishes are supported by a jointed series of arches which are collectively referred to as the visceral

skeleton. Similar structures are present in the embryos of land Vertebrates, but in the latter, except in a few salamanders, they persist in adult life only as vestigial elements supporting the muscles of the tongue and the voice-box. On either side of the skull one of these visceral cartilages, belonging to the foremost arch (Fig. 110), is connected by ligaments to the hind end of the chondrocranium and the angle of articulation of the jaw in the cartilaginous fishes. In the first fossil sharks there are several features which are not shared by modern ones. The pectoral and pelvic fins have broad bases and a row of spines occupies the space between them, suggesting the derivation of the paired fins by the segmentation of a continuous lateral fin on either side of the body, analogous to the dorsal and ventral fins. The other type of fishes found in the same strata are of the kind which are sometimes loosely called *Ganoids* on account of the character of their scales. They have left a few survivors to-day of which the sturgeons and lung-fishes are examples. In most respects they stand in an intermediate relation between the cartilaginous fishes and the true bony fishes, or Teleostei, in which the vast majority of fishes alive to-day are placed. The Teleostei, which do not appear till a much later date, have the surface of the body covered with thin plate-like scales of true bone. Small tooth-like scales are present in the leathery skin of the dogfishes and sharks, but these *denticles* are composed of dentine and enamel, and do not contain true bone. In the Ganoid fishes the body is covered with large, thick plate-like scales consisting of a layer of true bone with layers of dentine and enamel superimposed. The skeleton proper in some Ganoids which had persisted to the present day, like the sturgeons, may be completely unossified and essentially like that of the Chondrichthyes; but in the region of the head the scales form a continuous helmet of large bony plates. In all these earliest fish, both of the shark type and the sturgeon type, the body

or *centrum* of the vertebra (see Chapter II, p. 30) is tubular, so that there seems without doubt to have been, as in Cyclostomes, sturgeons and lung fishes to-day, a persistent unconstricted notochord (Fig. 111). In modern sharks and all bony fishes the centra undergo solidification, so that their articular surfaces only are hollow, and the notochord persists as isolated remnants between adjacent biconcave centra.

In the early Carboniferous we first find Vertebrates with five-fingered limbs, though suggestive impressions of foot-prints are found in the Devonian. These first Vertebrates, the *Stegocephali*, were like large salamanders. The exact stages which intervene between the fish fin supported by a large number of parallel cartilaginous or bony elements and the generalised pentadactyl limb (Fig. 117) are still obscure. But it is a characteristic feature of the Stegocephali that the limbs are small compared with the size of the trunk and do not project far outwards. The body could not have been lifted appreciably off the ground ; they waddled rather than walked. There is no abrupt discontinuity between the skulls and vertebræ of the Stegocephali and of those Ganoid fishes which already abounded in the Old Red Sandstone. In fact the skulls of the first land Vertebrates of the Carboniferous are far more like the skulls of the Devonian Ganoids than like those of any modern land Vertebrate.

In the Devonian we find abundant remains of a group of fishes with Ganoid scales, closely related on the one hand to the lung fishes, which in their circulatory and respiratory arrangements resemble those salamanders that breathe both by lungs and gills throughout life, and similar in many respects also to another small modern order (*Crossopterygii*) of fishes, represented by two fresh-water genera in Equatorial Africa (Polypterus and Calamoichthyes). The latter are characterised by fins with projecting fleshy bases whose skeletal elements are more suggestive of the axis of terrestrial

limbs than are the fins of other Ganoids. One fossil Crossopterygian (Sauripterus) has fin structures which are much more like the axis of a pentadactyl limb than are the fins of any modern fishes. Watson has brought out important similarities in the limb girdles of fossil Crossopterygii and Amphibia. Modern Crossopterygii, like the lung fishes, have true lungs, as well as gills, and breathe air.

The typical pentadactyl limb has characteristic features common to both the fore and hind member. The limb girdle of the first land vertebrates consisted of three paired elements, one dorsal and two ventral, pre-formed in cartilage. In the hind girdle they are respectively called the ilium (dorsal) which is attached to the sacral vertebrae, the ischium (posterior ventral) and pubis (anterior ventral). The fore limb girdle consists in the earliest land vertebrates with Amphibian or Reptilian affinities of a dorsal element, the scapula, and two ventral elements, one anterior, the pre- or epi-coracoid and one posterior, the coracoid. Neither of these ventral elements is present in typical Mammals, and only one is represented in birds and modern reptiles. In current text books this is usually designated the coracoid, but according to Broom, it corresponds to the precoracoid of the first land Vertebrates and Therapsids (*vide infra*). In the fore limb girdle there is a scale bone known as the clavicle not pre-formed in cartilage.

In the Ganoids of the Old Red Sandstone the internal skull had become converted into bone in the adult. The scaly plates of the head region tightly fit over the jaws, elsewhere remaining separate from the old skull, forming, as already remarked, a continuous bony helmet. So, too, in the first land Vertebrates the skull consisted of two portions —an internal bony part corresponding to the old cartilaginous skull of the dogfish and an outer armour of bony plates with only one pair of apertures, for the eyes. The most striking thing about the Stegocephalian skull is the

fact that these superficial bones are grooved and embossed exactly like the scaly armour of the head in the Ganoid fishes. The student should see this very characteristic feature in museum exhibits of the head of the sturgeon or the bony pike. The investing bones that fringed the jaws bore teeth.

The exact stages by which the ossification of the old skull took place are still obscure. Probably the first ossification took place in the region of the occiput and around the internal ear in the chondrocranium; the upper jaw ossifying at an early date to form the bone which is called the quadrate in Amphibia, Reptiles, Birds and bony fishes. A process of the quadrate cartilage also forms a bone called the epipterygoid or columella cranii of Reptiles. A corresponding bone incorporated into the brain case in Mammals is known as the alisphenoid. The articular head of Meckel's cartilage ossified to form the bone known as the articular in Amphibia, Reptiles and Birds. The bones which correspond to the quadrate and articular in the Mammalian skull will be mentioned later.

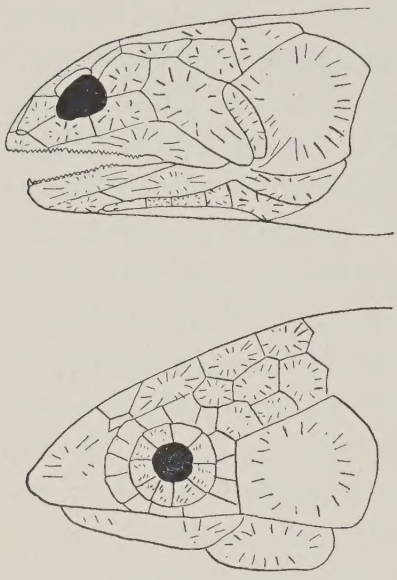

FIG. 112—HEADS OF TWO FOSSIL FISHES FROM THE DEVONIAN ROCKS. ABOVE: OSTEOLEPIS. BELOW: DIPTERUS

In such fossil Crossopterygii as Osteolepis (Fig. 112), related on the one hand to the air-breathing mud-fishes and on the other to the first Carboniferous Amphibia (Stegocephali) the chondrocranium was well ossified, and the elements in the skulls of the mammal referred to as supra-occipitals (in part at least), exoccipitals, basioccipitals, otics, basisphenoids and the anterior median ethmoid were

probably fixed before any vertebrates took to the land. In the Stegocephali the chondrocranium was completely ossified, so that the additional Mammalian bones known as the orbito- and presphenoids were in all probability represented in the first of the land-dwelling forms (Fig. 116). In modern Amphibia there is very little ossification of the chondrocranium : a ring-like bone in front (sphenethmoid),

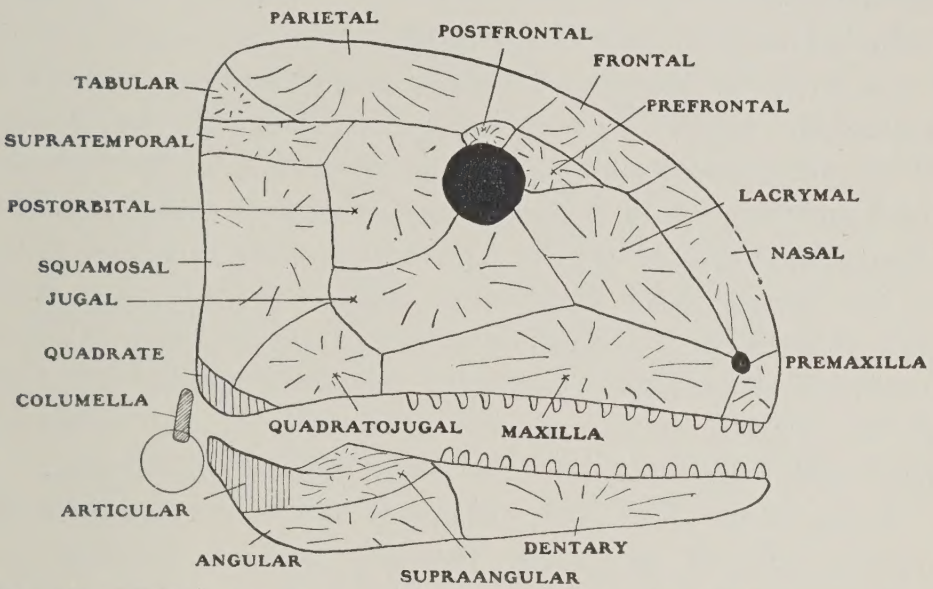

FIG. 113—THE SKULL OF A PRIMITIVE AMPHIBIAN (STEGOCEPHALIAN) OR REPTILE (COTYLOSAUR) FROM THE PERMIAN OR CARBONIFEROUS BEDS (Diagrammatic)

the otics and exoccipitals being the usual derivatives of the old brain case ; and in many living reptiles, such as the lizards, an analogous simplification exists, though the floor bones (basisphenoid and basioccipital) are still present.

In the fishes the hyomandibular was probably one of the first centres of bone formation in the old skull. With the consolidation of the jaw apparatus by the formation of an investment of scale bones, the hyomandibular dropped out as the effective link (or suspensorium) between the jaw apparatus and the upper part of the skull ; and it has ceased to play this rôle in the skull of the living lung fishes. About

the time when the first land Vertebrates appeared, the hyomandibular acquired a new significance. The land Vertebrates have a membrane—the tympanum or ear drum—stretched across the external orifice corresponding to the spiracle of the dogfish—now the eustachian tube; and the hyomandibular (now called the stapes or columella auris) serves to transfer vibrations from the ear-drum to the internal ear.

In the earliest Ganoid fishes the scaly plates of the head were, as in the Sturgeons to-day, very numerous, especially around the orbit. In such a form as Osteolepis the number of investing bones was with minor exceptions reduced to the fixed number found in the earliest Carboniferous Amphibia (Stegocephali) and earliest Permian reptiles (Cotylosauria). In the earliest land Vertebrates these investing bones were still superficial and quite separate from the bony internal skull. Moreover, they displayed the characteristic sculpture of the dermal armour of the head still seen in surviving fresh-water Ganoids like the bony pike (Lepidosteus).

These bones (Figs. 113, 114) were as follows: on the roof, paired tabulars, parietals, frontals, nasals; fringing the upper jaw of either side, quadratojugals, maxillæ bearing teeth and premaxillæ also bearing teeth; around the orbit postfrontals, postorbitals, jugals, lacrymals and prefrontals; linking the dorsal-aspect of the head to the angle of the jaw, supratemporals and squamosals; investing the outer-aspect of the lower jaw, the supra-angulars, angulars and dentaries (the latter alone tooth-bearing). To this must be added certain elements that are not superficial in location but arise nevertheless from the skin, not being preformed in cartilage. In the roof of the mouth there are three pairs of teeth-bearing bones, the palatines, transpalatines, and pterygoids, which invest the anterior end of the quadrate cartilage; anterior to these a pair of teeth-bearing scales known as the prevomers, and a median bone on the roof

of the mouth known as the parasphenoid. On the inner aspect of the lower jaw on either side there are three superficial bones known as the splenials, coronaries and the prearticulars. Of these elements the tabulars, supratemporals and postfrontals are not represented in any extant land Vertebrates.[1]

The Stegocephali had very short ribs attached to the transverse processes of the vertebræ, as have the salamanders.

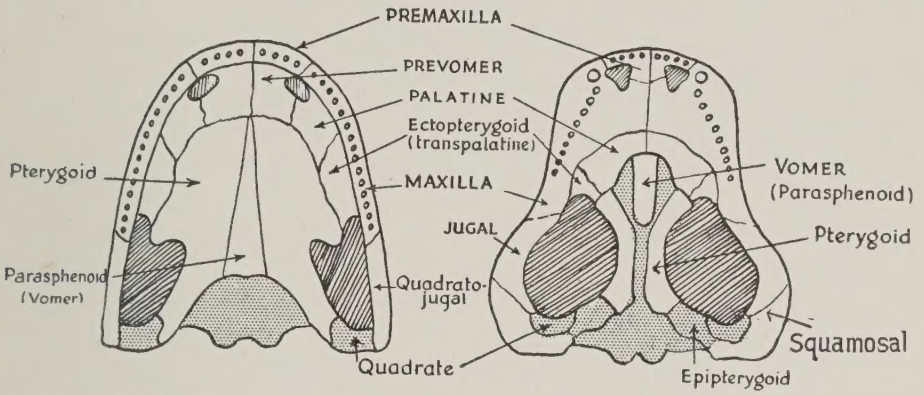

FIG. 114—THE PALATAL AND UPPER JAWBONES OF A STEGOCEPHALIAN OR COTYLOSAUR (PERMIAN) ON THE LEFT; AND OF A LATE TRIASSIC THERAPID REPTILE ON THE RIGHT

Their ribs did not form a bony chest like that of the reptiles, birds and mammals, in which they encircle the trunk in the thoracic region, meeting ventrally to form a sternum or breast bone. In the absence of a bony chest the Stegocephali resemble the modern Amphibia which approach more closely the fish organisation than do other land Vertebrates. But the skulls of modern Amphibia are much less like the skulls of a Ganoid fish than are those of the Stegocephali. The investing bones have no superficial resemblance to scales; they have sunk to a deeper situation, and are consolidated with the bones of the old skull, from which they are only distinguishable by the fact that they are formed by ossification of skin and not of the

[1] Whether a bone interposed between the parietal and squamosal of some lizards is the supratemporal or the tabular is not certain.

embryonic cartilaginous skull. Moreover, the number of superficial bones in the skull of a modern Amphibian is considerably less than in the Stegocephalian skull. In Urodeles the quadratojugals, postorbitals, supratemporals, postfrontals, and in some cases the maxillæ, are absent. In Anura all the circumorbital bones are absent, and the posterior elements of the lower jaw are fused to form an "angulosplenial." The vertebral centra of a few of the

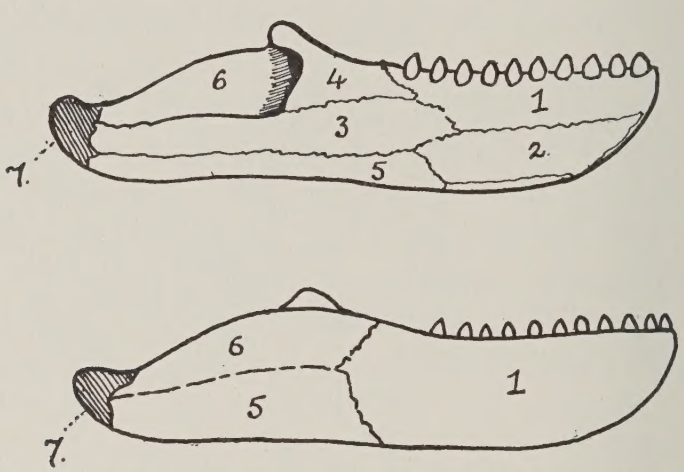

FIG. 115—THE COMPOUND LOWER JAW OF A REPTILE

Inner aspect above, outer below.

1—Dentary; 2—Splenial; 3—Prearticular; 4—Coronary; 5—Angular; 6—Surangular; 7—Articular.

earliest Stegocephali were tubular like those of the early Ganoids. In most forms they were of the biconvex type, as in some salamanders to-day. In frogs and toads, as in tortoises, crocodiles, and most lizards and snakes, the vertebral centra are solid, the convex posterior face of one fitting into the hollow anterior face of the next behind, so that the notochord is completely eliminated in adult life. The possession of tubular vertebral centra is a more generalised condition than is seen in any living forms, because it is a stage through which the axial skeleton of all land Vertebrates passes.

In the Permian there appear land vertebrates with more massive limbs and limb girdles provided with well-developed

ribs which practically invest the trunk to form a bony chest (cf. Fig. 118). These earliest Reptilian forms or *Cotylosauria*, of which Pariasaurus is an example, possessed a skull that was well roofed in and had an aperture for the eyes only. But it is more solid and compact than that of the typical Stegocephalian, and the superficial bones though still grooved are less obviously like scaly plates.

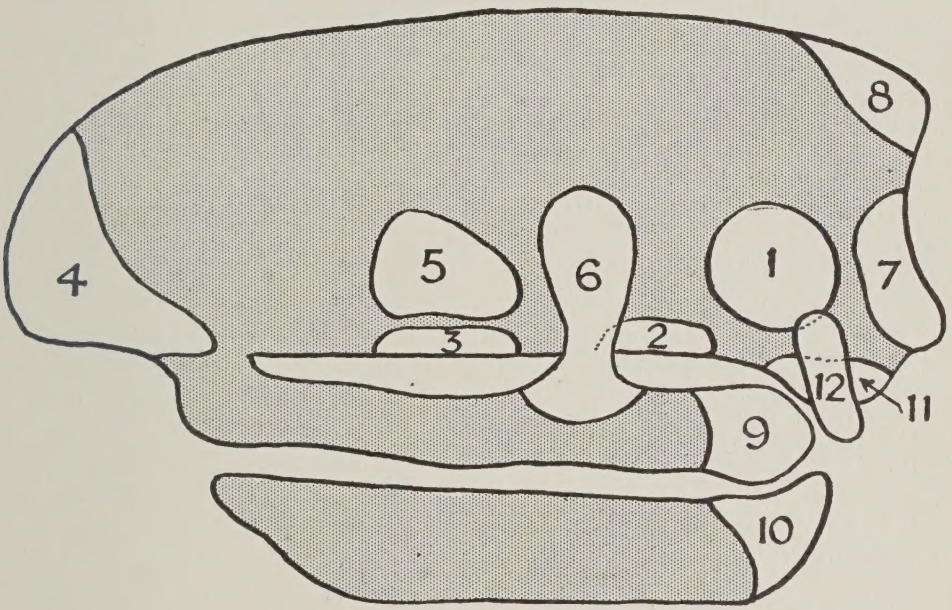

FIG. 116—THE CHONDRIAL BONES OF THE MAMMALIAN SKULL

1—Otic; 2—Basisphenoid; 3—Presphenoid; 4—Ethmoid; 5—Orbitosphenoid; 6—Alisphenoid (=epipterygoid); 7—Exoccipital; 8—Supraoccipital; 9—Incus (=Quadrate); 10—Malleus (=Articular); 11—Basioccipital; 12—Stapes (=hyomandibular or columella auris).

The Cotylosaurs for the most part incline more to the Mammalian type of skeleton in one respect inasmuch as the pelvic girdle is tilted slightly backwards rather than forwards. From the lower to the upper Triassic beds, we can now trace a series of forms which show increasing approximation to the Mammalian type of skeleton in every particular. The series is referred to by the term *Therapsida* or *Theromorpha* and is abundantly represented by well-preserved remains

in the Karroo deposits, recently studied by Broom, Watson and Haughton.

The Mammalian skull is the most distinctive feature of the class Mammalia, and as we have only referred to the diagnostic features of the soft parts, a few words must here be inserted to distinguish the skulls of Mammals from those of Reptiles (Fig. 119), Birds and Amphibia. The main points to be noted are as follows : (1) With the enlargement of the

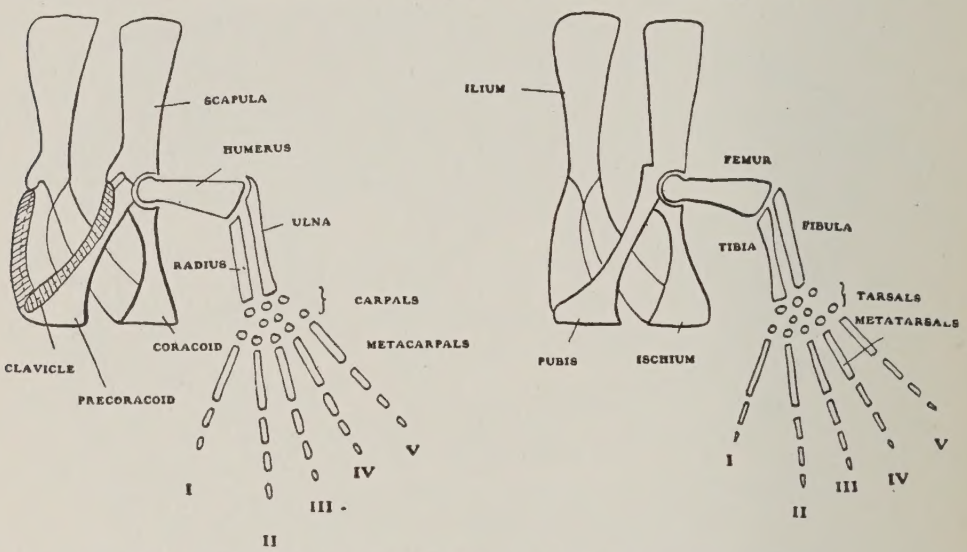

FIG. 117—THE PENTADACTYL LIMB AND ITS GIRDLE

Left, Fore limb. *Right*, Hind limb. The head end of the animal is towards the left.

brain which attains its maximum development in the Mammalia the brain cavity has expanded upwards, so that the squamosals take a share in the lateral wall of the brain case, the otic bones become ventrally displaced below them, and the parietal bones which are typically flat in reptiles become arched and often crested for the insertion of the more powerful jaw muscles; (2) In the temporal region there is a widely open fossa which generally includes the orbit and is bounded by a laterally projecting cheek bone, the zygomatic arch, formed by the union of the jugal and squamosal; (3) The lower jaw is a single bone, typically projecting upwards under the cheek bone and articulating

against the squamosal, so that quadrate and articular bones so conspicuous in reptiles and birds are absent from the jaw articulation; (4) Two small extra bones—the incus and malleus, arising like the quadrate and articular from the embryonic cartilaginous jaw elements supplement the columella or stapes as ear ossicles (Fig. 121); (5) The teeth, less numerous than in Reptiles, are differentiated as cutting (incisors), tearing (canines), grinding (premolars and molars) series.

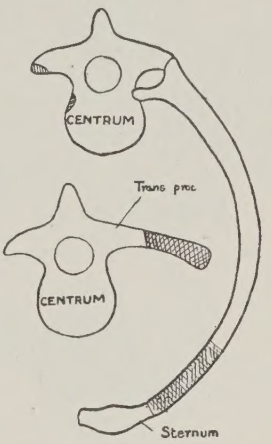

FIG. 118—RIB AND STERNUM OF A MAMMAL (right), AND CARTILAGINOUS RIB OF A SALAMANDER (left)

Early members of the Therapsid series (Fig. 119) such as Moschops, which appear in the Upper Permian, show a more decided tendency in their limb structures to lift the body well off the ground, than did the Cotylosaurs. The backward tilt of the pelvic girdle is more pronounced. In the skull the only noticeable innovation is the appearance of a large vacuity in the investing bones at the side of the head, bounded by the postorbital, jugal and squamosal bones. The appearance of this vacuity heralds the emergence of a very mammalian feature seen increasingly in the skull of middle and upper Triassic forms, namely the bulging outwards of the cheek region to form the characteristic mammalian zygomatic arch. In the next stage we see two new features well represented in a form like Lycosuchus, first the increasing size of the dentary which now sends back under the projecting cheek bone a large process, and secondly the beginnings of a carnivorous type of dentition. In the late Triassic Theromorphs like Cynognathus, Gomphognathus and Galesaurus, the differentiation of the teeth into incisors, canines and molars is definitely mammalian, but even more important are two other features which respectively concern the jaw articulation and the

palate. As regards the former we find that the accessory jaw elements, now on the point of disappearing, are loosely applied to the inner surface of the dentary, which has encroached so completely upon them that its posterior

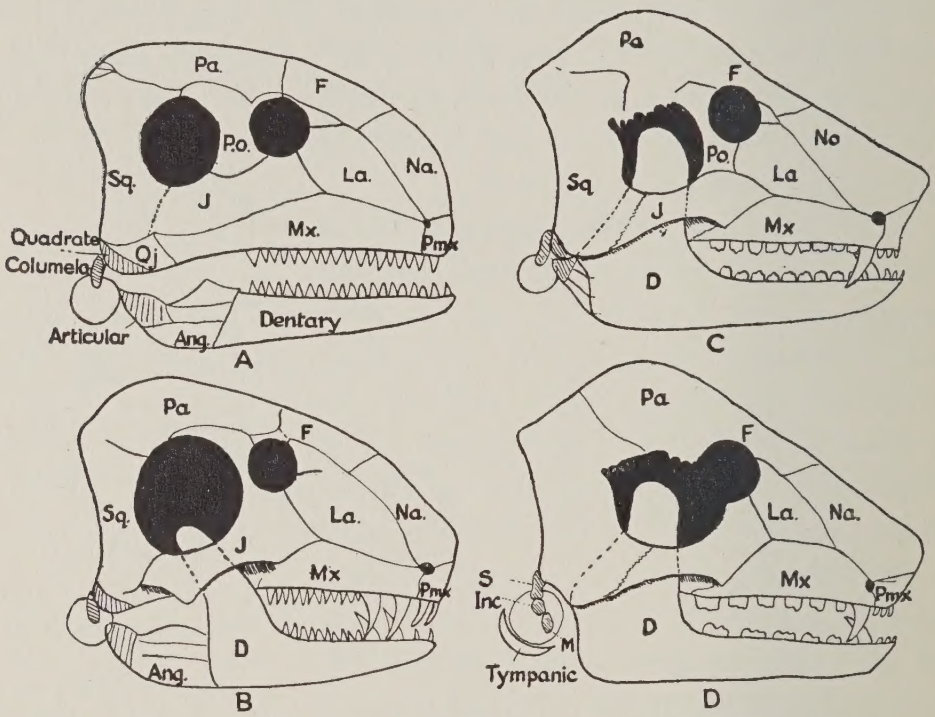

FIG. 119—COMPARISON OF SKULLS OF REPTILES AND MAMMAL (Diagrammatic)

A—Upper Permian Therapsid; B—Lower Triassic Therapsid; C—Late Triassic Therapsid; D—Mammal. See Fig. 113 for names of bones.

margin practically rests against the squamosal, and the quadrate and articular are ceasing to constitute the effective jaw articulation. With reference to the palate we find that in the late Theromorphs like Cynognathus, with well developed carnivorous specialisation, the maxillary and palatine bones send inwards plates which meet in the middle line below the narial aperture, forming the type of palate which is found in Mammals but is not peculiar to them. In some Theromorphs (the Gorgonopsids), the parasphenoid, which in Mammals forms a septum in the narial passage called the " vomer," is found to have shifted forwards into the palatal region.

Indisputable mammalian remains occur in the early Jurassic and probably at the end of the Triassic. In the true mammalian skull the quadrate and articular have completely dropped out of the jaw articulation, and they are represented by two additional ear ossicles; the lower jaw consists of dentary alone, the quadratojugal and post-orbital have disappeared, and along with them, except in Monotremes (*vide infra*), have gone the prevomers and the prefrontals.[1] We have confined ourselves to the more striking transitional features of the skull in the Anomodont reptiles. Other points which might be mentioned are that the top of the skull becomes more arched and the brain case larger as we pass up the series. We have mentioned that even in the earliest members of the series the hind limb and its girdle incline to the mammalian type. As regards the fore limb, Mammals as a whole differ from the first Reptiles in the complete absence of coracoids and precoracoids, but the gulf in this case is bridged by the Australian order called *Monotremata* which comprises two genera, Ornithorhynchus, the duck-billed platypus, and Echidna, the spiny anteater. These differ from all other Mammals in laying eggs like the eggs of Birds and Reptiles and also in the fact that the shoulder girdle (Fig. 120) has large coracoids and precoracoids meeting the sternum with a large T-shaped median bone called the interclavicle, very characteristic of the reptilian shoulder girdle. In Mammals

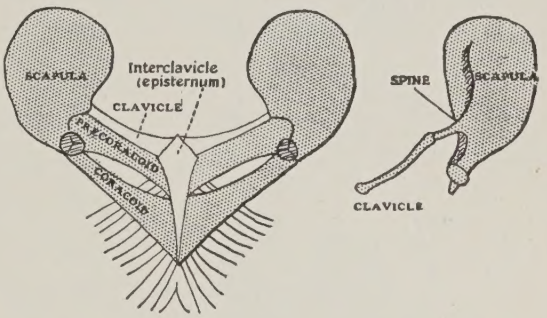

FIG. 120—SHOULDER GIRDLE OF A MONOTREME (left) AND TYPICAL MAMMAL (right)

[1] An extra bone in mammals known as the *tympanic* surrounds the middle ear.

generally the margin of the scapula with which the collar bone articulates is deflected outwards to form a lateral spine. This is also seen in forms like Cynognathus, where the shoulder blade approaches the characteristically mammalian trihedral shape. As regards the axial skeleton there are no points that call for special attention. The vertebral centra of the Cotylosaurs are of the biconcave

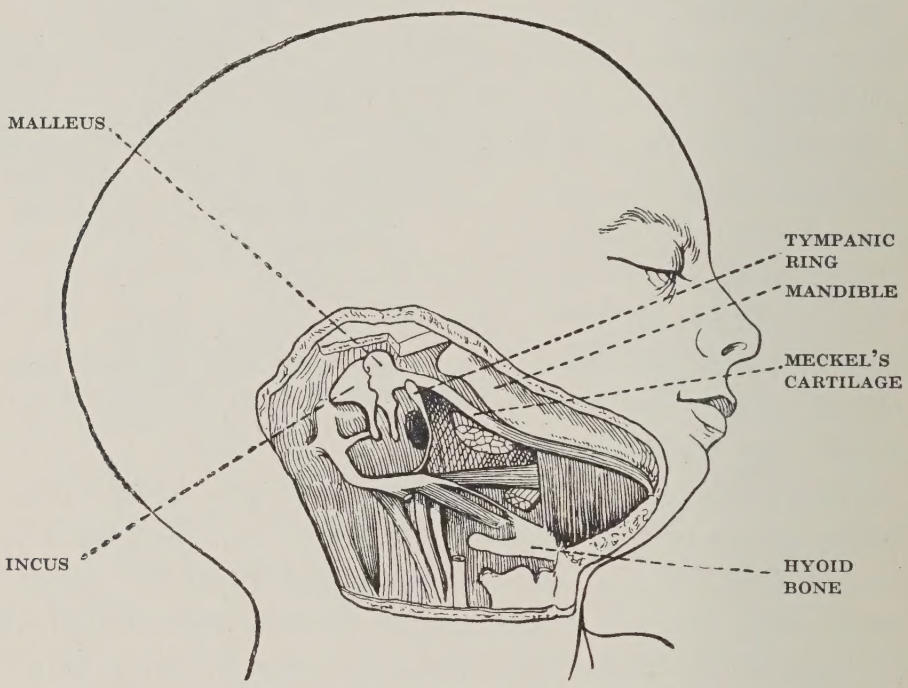

FIG. 121—HEAD OF HUMAN FOETUS
Showing the two extra ear ossicles: Malleus (articular) and Incus (quadrate).

type. In the late Theromorphs the articular facets are flatter. In Mammals they are quite flat, so that the notochord does not persist at all in adult life. The number of neck vertebræ in Cynognathus and in Mammals is fixed (seven), and the fact that it is identical in the whale and the giraffe affords an excellent illustration of Unity of Type. In the Platypus there are vestigial cervical ribs; in other Mammals they are completely fused with the vertebræ, but the interspace between the two heads of the rib persists as a canal on either side of the vertebra.

At the end of the Permian we find representatives of an order of Reptiles (*Rhynchocephalia*) which have left one survivor in modern times, the New Zealand lizard, Sphenodon. They differ from the Cotylosaurs in one striking particular, the presence of two large vacuities at the side of the skull, one like the temporal fossa of Moschops between the postorbital, squamosal and jugal bones, and one between the postorbital, squamosal and parietal bones, so that the side of the head has two conspicuous bony arcades. Other minor points are the tendency as in all modern reptiles for the pelvic girdle to be tilted forwards, and the presence, as in birds, of prominent projections (uncinate processes) on the posterior margin of the ribs. From the early Triassic Rhynchocephalia we can trace series leading in different directions. One important line of specialisation is characterised by the large development of the hip girdle with a broad extension of the ilium forwards and behind the thigh socket. This is characteristic of the *Dinosaurs*, an order which attained tremendous importance in the Cretaceous and died out. Many of its members were bipedal, and closely allied to the Dinosaurs were the flying reptiles or *Pterodactyls*, in which the enormously enlarged fifth finger supported a wing membrane. In some of the small Triassic Dinosaurs the limb bones were

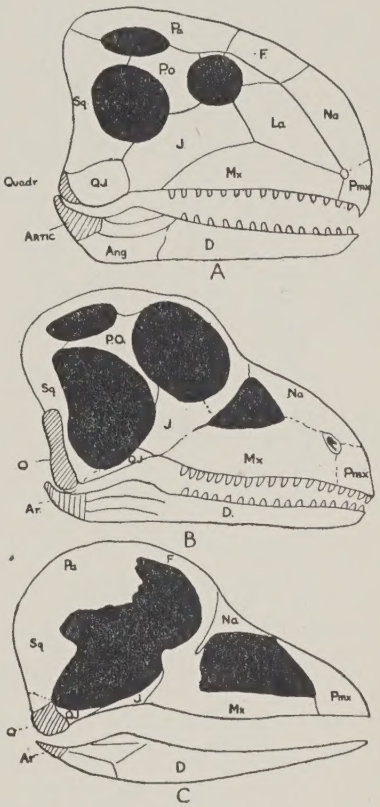

FIG. 122—SKULLS OF A. RHYNCHOCEPHALIAN (PERMIAN); B. DINOSAUR (JURASSIC), AND C. MODERN BIRD—diagrammatic

hollow as in birds. The character of the hip girdle of Dinosaurs is unlike that of any modern reptiles, but closely resembles that of birds. The skulls of Dinosaurs had the two large temporal vacuities of the Sphenodon skull, but in addition, as in birds, there were large vacuities in front of the orbit. Moreover, in some of the Triassic Dinosaurs (*e.g.* Anchisaurus) the postorbital bones and the lower temporal arcade were very slender, so that apart from the presence of the former, which has disappeared in birds, the skull is essentially avian. Not only in the hip girdle but in the hind limb itself do we find avian features. Taking birds as a whole, including Archæopteryx, one of the most characteristic features of their skeleton is the fact that the distal tarsals and all the metatarsal elements are fused into one bone (tarsometatarsus). This feature is actually realised in one or two genera of early Dinosaurs such as Ceratosaurus. In the upper Jurassic, Archæopteryx, the feathers of which have left perfect impressions in the slate, appears. This primitive bird had a long tail like a lizard and the fore limb had three well developed digits (Fig. 124) with claws like the fore limbs of the bipedal Dinosaurs. Archæopteryx had teeth and so had the birds of the Cretaceous epoch, and the Cretaceous birds had, like the Rhynchocephalia and Dinosaurs, biconcave centra as opposed to the characteristic saddle-shaped vertebral centra of modern birds.

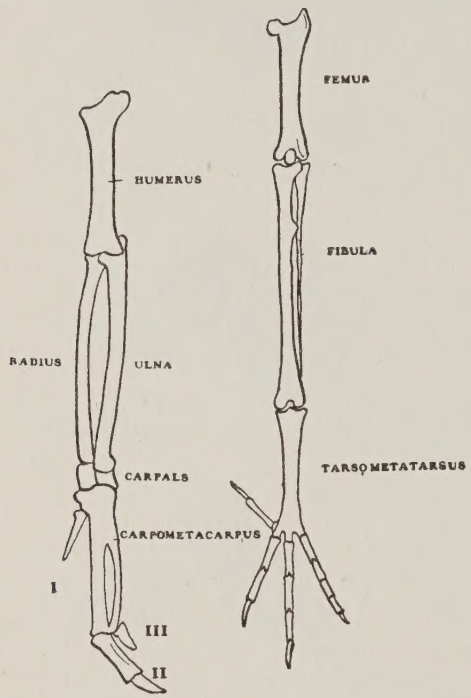

FIG. 123—LIMB SKELETON OF A BIRD

One series of forms connects the Rhynchocephalia with the crocodiles. This series is well represented in the Triassic and Jurassic strata. The main points concern the elaboration of the characteristic false palate of the crocodiles, in which the pterygoids as well as the palatines and maxillæ participate to shift the internal narial aperture far backwards. In addition we see the progressive solidification of the vertebral centra. A false palate of the mammalian type is also seen in the tortoises, the earliest members of which go back to the end of the Permian, and possessed a skull without any lateral vacuities like that of the Cotylosaurs. Some tortoises share with two wholly fossil aquatic or semi-aquatic orders, the *Plesiosaurs* and *Ichthyosaurs*, a vacuity in the temporal region corresponding to the lower one in the skull of Sphenodon. The stages which connect the tortoises with the early reptilian stocks are not yet elucidated, and in one respect the story is discontinuous in that the pectoral girdle of tortoises lies inside the ribs. It is noteworthy, however, that the Chelonian stock was emerging before the complete investment of the thoracic region was effected. Lizards and snakes which are the most successful modern Reptilia appeared last of all. The distinctive feature of this order of reptiles (*Squamata*) is the fact that the quadratojugal has disappeared, so that the quadrate is moveable. The lower arcade of the Sphenodon skull is thus absent. There is an upper arcade in most lizards, but with the elimination of the postorbital bone this has disappeared in the snakes.

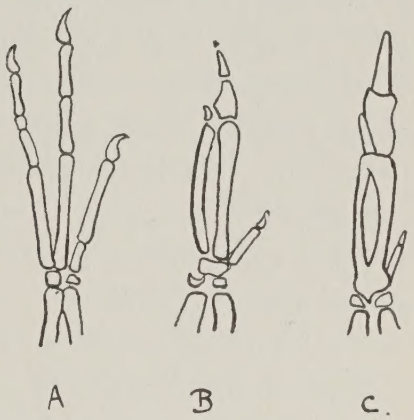

FIG. 124—DIGITS OF FORE LIMB OF ARCHAEOPTERYX (A); SIXTEEN-DAY CHICK (B); ADULT FOWL (C)

The task of elucidating the details of structure in fragmentary remains is often a difficult one, and the student may justifiably be tempted to surmise that a good deal of imagination is incorporated in the sometimes fanciful reconstructions that are figured in many semi-popular works. Nevertheless, there are certain broad general conclusions now well accredited by well-nigh complete skeletons of a large number of fossil genera and supplemented by innumerable less complete remains which confirm them. We know almost as much about the skeletons of Pariasaurus, Archæopteryx, Cynognathus, for instance, as we do about that of a living vertebrate. Laying aside speculative interpretations and exaggerations the following points are sustained by ample data :—

(1) That there existed a time when the only vertebrates were of the Piscine type ;

(2) That previous to the appearance of land vertebrates there existed fish which resemble those fish which most nearly approach the land vertebrates in their respiratory and circulatory arrangements ;

(3) That the first land vertebrates with terrestrial limbs in the early Carboniferous have skulls of which the superficial bones are scaly plates like those which cover the head region in the Ganoid fishes ;

(4) That there appeared at a later date, in Permian times, Reptilian forms with large limbs and a bony chest, animals that no longer waddled but lifted the body well off the ground ;

(5) That during the time intervening between the appearance of the first Reptiles and the emergence of true mammals and birds in the Jurassic there existed reptiles which in every feature of their organisation show bird-like or mammal-like characteristics seen neither in modern reptiles nor in the Permian forms.

The student will find in other works more detailed accounts of the subsequent specialisation of birds and mammals,

illustrating for instance the modification of the skull in the fossil whales, the reduction of the toes and elaboration of the grinding teeth in horses and camels. The broad general outline which has been given above must suffice to illustrate the Principle of Succession for the present purpose and, though amplified by much evidence that has accumulated since Darwin's time, it indicates the view to which the study of fossils had pointed by the middle of the nineteenth century.

Geographical Distribution. We have seen that the gaps between living animals are to a remarkably striking extent filled in by intermediate forms which lived on this earth in past epochs, and, taking into consideration the inevitable incompleteness of the geological record, we are driven to envisage a continuous succession of organisms with increasing divergence of structure in the history of life on our planet. Before we can appreciate precisely how continuous this succession has been, we have to take into account the fact that the same animals are not found in all the different parts of the globe. One group of animals may be confined, like the kangaroos, to Australia, one group, like the aardvark, a mammal peculiar enough to be put in an order by itself, to South Africa. If, then, we know that there existed in, let us say, Jurassic times, a small mammal which was of a type so generalised as to form a link between the kangaroo and the aardvark, it is clearly of interest to enquire whether the barriers of ocean that now separate Australia and South Africa were as impassable in Jurassic times, or whether this archetypal mammal lived in a situation from which it could have access equally to two such promising lands of settlement for its family. To put the issue in more general terms, was the process of geological succession a continuous one both in time and space?

To answer this question demands a brief survey of the

existing distribution of animal life on the earth, perhaps the most significant contribution that Darwin and Wallace made to the evolutionary hypothesis. It was in their writings that the facts of geographical distribution (facts which were very largely based on their own first-hand observations, and not like their erroneous views upon heredity collected from the testimony of other persons) first received critical examination. At the outset they saw that no amount of ingenuity could successfully interpret the geographical distribution of animals on a teleological basis. The habitat of different kinds of animals is not uniquely determined by their special fitness for the locality in which they occur. This statement is attested by innumerable instances of species that have formerly been restricted to a very definite area, but when introduced into other parts by man have flourished phenomenally, as in the case of rabbits in Australia. New Zealand with no indigenous wild mammals has now, though it has only had access to the outer world for one hundred and fifty years, no less than twenty-five species of mammals living freely in the wild state. We have, therefore, to seek for some more material explanation of the facts than the argument from Paley's watch. In the *Origin of Species* Darwin deduced two main conclusions. These may be stated briefly as follows :—

(1) The extent of distribution of species is in general greater, if their means of dispersal is greater. The Amphibia, to which the frog belongs, are a group which are never represented in oceanic islands, that is to say, islands which are separated from mainland by great depth of ocean. They are dependent on fresh water, and are not able to withstand drought ; they do not form resistant eggs, or encysted embryos which can be carried by birds or by wind, as are so many small fresh-water organisms. Moreover, the Urodela or tailed Amphibians, which include the salamanders, a group more characteristically

aquatic than the Anura or frogs and toads, is unrepresented in Africa south of the Sahara desert. Terrestrial mammals do not occur on oceanic islands, but bats are much more cosmopolitan in this respect.

(2) The inhabitants of islands are more closely similar to the inhabitants of the nearest mainland than to more distantly remote regions. This is particularly striking in the case of the resemblance of two groups of volcanic islands, the Galapagos and Cape Verde Islands to the American and African Continents respectively. Moreover, the proportion of species on oceanic islands which are peculiar to them is very much greater than in the case of islands recently separated from the mainland. Both these conclusions are well illustrated by the butterflies and moths of New Zealand. Of 1,040 species of Lepidoptera in New Zealand, according to Thomson, 63 are Australian, 24 cosmopolitan and the remainder unique.

The following tables taken from Romanes, though requiring some amplification in view of more recent systematic research, are still representative. St. Helena, Galapagos Islands and the Sandwich Islands are typical oceanic islands separated by a great depth of water from the mainland. The British Isles were in glacial times connected with the mainland of Europe. The British Isles include about a thousand islands large and small. St. Helena is a single volcanic rock.

A. Peculiar or Endemic Species.

	Land molluscs.	Insects.	Reptiles.	Land birds.	Mammals.
Sandwich ...	400	?	2	16	0
Galapagos ...	15	35	10	30	0
St. Helena ...	20	128	0	1	0
British Isles ...	4	149	0	1	0

B. Non-peculiar Species.

	Land molluscs.	Insects.	Reptiles.	Land birds.	Mammals.
Sandwich ...	0	?	0	0	0
Galapagos ...	?	?	0	1	0
St. Helena ...	0	?	0	0	0
British Isles ...	83	12,551	13	130	40

We see, then, that the following rule may be stated: the more geographically isolated different animals are the more anatomically distinct will they generally be found to be. This is a statistical rule.

The converse is also true if we study any restricted group. To take as an example the South African scorpions, we find independently of climate and habit that the scorpion of Cape Town is more like the scorpion of Cairo than the scorpion of Colorado. Six families of scorpions are commonly recognised. If we exclude the neighbourhood of the Suez and a small part of Morocco only two are represented in the African continent, the Scorpionidæ and the Buthidæ. Both these families are represented throughout the East, South of the Himalayas, in South America and in Australia. There are three genera of Buthidæ in Cape Province. Of these, the commonest in the Cape Peninsula, Uroplectes, is restricted to the region South of the Equator. Parabuthus extends up along the Nile valley across the Suez peninsula into Arabia but not into North-west Africa. Buthus ranges over the entire African continent and throughout South Asia. None of these genera extend into America or Australia. Of the Scorpionidæ the only Cape genus is Opisthophthalmus which is restricted to the portion of Africa south of the Great Lakes. Thus, of four genera of scorpions in the Cape, two will be found to be represented near Cairo, one near Calcutta and none in Colorado.

To the above remarks it is necessary to add that the most ancient living representatives of any group tend to have the most strikingly discontinuous or, on the other hand, widely spread distribution, while groups which have a very discontinuous distribution at the present day are generally found to have had a more continuous distribution in the past. Moreover, the fossil remains found in any region are closely related to the faunistic features of that region.

Of recent years the attempt has been made by Willis to extend the study of geographical distribution by quantitative treatment. Willis' work, however, deals more especially with plants rather than with animals, and at present the problem of animal distribution has been insufficiently investigated by exact methods to merit further discussion. What is known, however, lends support to the extension of the principle of geological succession with which the name of Wallace is especially associated. Wallace's law (1855) is thus briefly stated at the conclusion of the paper entitled *On the Law which has Regulated the Introduction of New Species* :—

> Every species has come into existence coincident both in space and time with a pre-existing closely allied species.

With the statement of this law, and its documentation with more carefully sifted and comprehensive data, the positive contribution of the nineteenth century to the development of an objective theory of evolution ended. Biology had made immense strides forward during the period that intervened between the speculations of Lamarck and his contemporaries on the one hand and the publication of the *Origin of Species* on the other, and it is easy to see how acceptable to biological thought any hypothesis which could interpret the phenomena of Succession in terms of a natural agency must have been. But at that time Mendel alone clearly saw the importance of a study of the nature of

the agency by which new anatomical characters are handed on from generation to generation. The hypothesis that Darwin put forward satisfied the requirements of contemporary knowledge. But the supreme contribution of Darwin lay in amassing with masterly skill the accumulated fruits of the researches of the first half of the nineteenth century, and in demonstrating the enormity of the task to which those who advocated a teleological view of creation were committed. The picture of a progressive gradual differentiation of animal life as it spread over different parts of the earth in successive geological epochs became an integral part of the naturalistic outlook. It remained for the Mendelian Renaissance to clarify the conception of this gradual differentiation as an outcome of the agency of natural generation.

NOTE

The nomenclature of Vertebrate osteology is still in a state of confusion owing to the fact that names employed in human anatomy were extended to bones of other vertebrates, before the study of palæontology had progressed to its present dimensions. If the mammalian condition is taken as the standard, the palato-pterygo-quadrate bar should be called the alispheno-quadrate, since it corresponds to the mammalian alisphenoid and the quadrate of land vertebrates. The palatines and pterygoids are not formed by ossification of the " dogfish jaw." The bone known as the alisphenoid in crocodiles seems to correspond to the orbitosphenoid of Mammals, and the sphenethmoid of Amphibia probably corresponds to the presphenoid of Mammals. The bone known as the vomer in Mammals is the parasphenoid of fishes, Amphibia and reptiles, and the rostrum plus basitemporal of birds. The bones known as vomers in Amphibia, reptiles and birds should henceforth be called prevomers. Probably the coracoid of modern reptiles and birds is equivalent to the precoracoid of Therapsids and Monotremes. The views stated in the foregoing summary are largely due to the work of Broom and Watson.

Chapter XII

THE PRINCIPLE OF GENETIC VARIATION

WE now reach the final step in the argument which it has been our aim to build up during the preceding four chapters. We have formulated in Chapter VIII a problem. That problem was, by what natural process has the existing diversity of living matter in its innumerable specific manifestations come into being? Assuming that living matter with its characteristic reactivity, receptivity and reproductivity exists, how does it come about that living matter is met with in so many different forms which we refer to as species? We have studied the problem as far as practicable in its historical setting, because that method of presentation alone leads to a clear perspective of the methodological aspect of the Evolutionary Doctrine, and enables us to approach it as a logical construction. This task is not one that can be undertaken without clearing away a good deal of confused thinking still current not only in popular science but in most biological textbooks. We read of the Evidence from Anatomy, the Evidence from Embryology, the Evidence from Geology, and so forth. But no facts of anatomy, geology or embryology *taken alone* justify the evolutionary hypothesis. The weaving together of certain principles derived from anatomy, embryology and geology *in the light that experiment throws on the nature of the reproductive process* constitutes the completion of the evolutionary argument.

Let us be clear, then, about how much we have proved up to this point. First, that living animals only come into

being in our immediate experience through the agency of natural generation. Second, that the degree of similarity which animals display in their hereditable properties must be interpreted primarily in terms of the hereditability of the properties themselves, and not in terms of a purposive agency. Third, that there is abundant evidence of a gradual and accumulative divergence in the hereditable properties of animals continuing over vast geological epochs. It remains, therefore, to interpret this divergence in terms of the only agency through which living matter is brought into being in our experience. This brings us to the fourth step in our argument, the enunciation of the Principle of Genetic Variation, which concerns itself with the experimental fact that units of living matter with new hereditable properties do actually come into being in the normal operations of the process of natural generation. Thus in the final analysis the evolutionary argument rests on the testimony of experiment, and we may state the conclusion of our investigation in the following terms. Animals with new hereditable properties have appeared successively with increasing divergence of type in the past history of the earth; animals only arise in our experience by reproduction from pre-existing animals; animals with new hereditable properties can arise in our immediate experience by reproduction from pre-existing animals with different hereditable properties; therefore it is natural to conclude that the existing divergence of specific characteristics is the outcome of a natural process operating over long periods of geological time.

Before asserting this conclusion with too great a measure of confidence, it would be well to examine more closely the implications of the Principle of Genetic Variation and this may conveniently be done by proposing four questions: first, whether the origin of new hereditable types under experimentally controlled conditions is an

established fact; second, whether any natural agency ensures that new types having so arisen will be preserved; third, whether the appearance or preservation of new types is an occurrence of sufficient frequency to have accounted for all the divergence of specific form that has come about in the interval of time which geology places at our disposal; and lastly the nature of the species barrier.

Origin of New Hereditable Types. Thirty years of controlled experiment on the lines laid down by Mendel's work has given abundant proof that there do arise occasionally in pure stocks individuals with new hereditable properties. Such individuals are called *mutants*, a term which is used synonymously by some writers with the alternative word "mutations." As the word "mutation" was originally employed by de Vries in a somewhat different sense from that in which the term "mutant" is used, it is preferable to avoid perpetuating this confusion. A new phase in this aspect of the evolutionary problem has lately been opened up by the work of Muller, who with exposure of individuals to X-rays has produced mutants in Drosophila by a controllable agency.

To Darwin and Wallace is usually given the credit of first emphasising the fact of genetical variation. But in reality it was not until the publication of de Vries' *Mutation Theory* and Bateson's *Materials for the Study of Variation*, in the nineties, that the way was paved for a clear recognition of the reality of genetic variation, and the imperative necessity of putting the issue to experimental test. Lest there should be any doubt about this point the following citations from the *Origin of Species* (in which the italics are inserted) will be amply sufficient to make clear what Darwin himself meant by "the origin of species by Natural Selection":—

Any being, if it vary in any manner profitable to itself, under the complex and sometimes varying conditions of life, will have a

better chance of surviving, and thus be naturally selected. From the strong principle of inheritance, any selected variety will tend to propagate its new and modified form. (From the Introduction.)

Variations, *however slight, and from whatever cause* proceeding, if they be in any degree profitable to the individuals of a species, in their infinitely complex relations to the individuals of a species . . . will tend to the preservation of such individuals and will generally be inherited by the offspring. The offspring also will have a better chance of surviving, for, of the many individuals of a species which are periodically born, but a small number can survive. *I have called this principle, by which each slight variation if useful is preserved, by the term Natural Selection.* (Chapter III.)

The fundamental difference between the conception of variation employed in the *Origin of Species* and the modern idea of genetic variation will at once be seen by going back to one of Mendel's classical experiments (p. 142). The individuals of the dwarf and tall class of peas in our initial experiment are not all alike. Any dwarf shoot grown under ordinary conditions is distinctly smaller than a tall shoot, so that the two classes are discontinuous and quite easily distinguishable. Even when the conditions are standardised as much as possible, however, small differences of light, moisture, soil-content, temperature or proximity to one another play their part, so that no two dwarf plants are of exactly the same size. What is transmitted through the gametes is something which determines the extent to which an individual is capable of growing under appropriate conditions.

It is perfectly clear from the citations given above that Darwin, like Wallace, used the term " variation " to include not only genetic variation, *i.e.* the production of mutants as defined above, but differences between parents and offspring of whatsoever character. In short, the overwhelming majority of differences between parents and offspring to which they applied the term "variation" were of bodily, rather than germinal, origin, and as such have nothing to do with

problem of evolution unless, as Darwin himself did, we accept the Lamarckian doctrine.

Weismann, writing after the discovery of the fertilisation process, thus defines the conception of variation, which corresponds with that of Romanes and other selectionist writers of the period :—

> Heredity is the transmission of the physical nature of the parent to the offspring. We have seen that this transmission affects the whole organism, and extends to the most trifling details, and we also know that it is never complete, and that the offspring and parent are never identical, but that the former always differs more or less from the latter. These differences give rise to the phenomenon of *variation, which thus forms an integral part of heredity, for the latter always includes the former.* (*The Germ Plasm,* p. 410.)

Though Darwin treated Lamarck's speculations with scant respect, it is indisputable that the Lamarckian principle was just as truly implicit in his theory of natural selection as in the earlier views of his grandfather, Erasmus Darwin, Goethe, St. Hilaire and others, contemporary with Lamarck. And when the Lamarckian principle was rejected by Wallace, following the lead of Weismann, the natural selection theory crystallised into a more rigid form, which we shall have to discuss later.

There are still students of fossil forms who claim that the Lamarckian principle is necessary to explain the historic succession of animals by continuous generation. There seems to be no adequate reason to justify the statement that evolution cannot be satisfactorily explained without assuming the inheritance of acquired characters. But if there were it would not be an argument in favour of the Lamarckian principle so much as an argument against the evolution theory, since it would imply that the truth of evolution depends on assuming a mechanism for whose existence we have insufficient evidence. The fossil record again and again

gives evidence of the part which inheritance of size differences has played in the history of animal life in the past, and the disposition to favour the Lamarckian view that one notes among palæontologists, from the time of Cope to the present day, seems to be influenced by this consideration. Recent research, as we have seen (p. 175), however, encourages us to believe that inheritance of size, which at first baffled Mendelian methods, is subject to the law of segregation, and as we come to recognise more and more the dependence of hereditary transmission on discrete particles which maintain their entities uncontaminated through all the cell divisions of the body, segregating in their entirety during the formation of gametes, the unlikelihood of the Lamarckian principle becomes more and more evident. Indeed it is legitimate to state not merely that the assumption of the principle is gratuitous, but its probability is so small as to necessitate the most imperative and spectacular evidence before enlisting further interest in it.

If we attempt to analyse in exact terms the belief that "acquired characters" are inherited, it appears to involve two separable issues, (*a*) whether the inhibition or destruction of a character is accomplished wholly or partially by the destruction of its material antecedent in the germ cells, or (*b*) whether, if a stimulus of a given magnitude is required to call forth a given response, the application of that stimulus to the parent carries with it the possibility of evoking the corresponding response in the offspring with a stimulus of smaller intensity. Without committing oneself to a dogmatic negative, it can be stated as a matter of fact that in a good many cases the answer to both questions is certainly in the negative (within the limitations of experiment on these lines), and that in no single instance where a positive answer has been given, has independent and rigorous reinvestigation confirmed the observations recorded. The principle of "economy of hypothesis" is therefore best

preserved if the 'Lamarckian' principle is eliminated from consideration.

It may be said that until Mendel's work gained recognition heredity and variation were not experiences to be investigated but axioms to be accepted. It is just those propositions which everyone accepts that the scientist is most anxious to examine in the hard light of experience. In attempting to envisage a natural mechanism by which the graded differentiation of animal structure could have been brought about, Lamarck was content to take for granted the generally accepted belief in the inheritance of acquired characters without bringing it to experimental test. Darwin, fortified with newer knowledge of the historical succession of animals and plants as recorded in the rocks, sought to show that evolution was a consequence of competition and the "strong principle of inheritance." In fact, he did not undertake the task of enquiring into the nature of the strong principle of inheritance. Mendel alone at this time saw the necessity for an experimental study of inheritance, and pointed the way to a non-dialectical treatment of the problem.

Till the influence of the writings of de Vries and Bateson began to be felt in the nineties the evolution theory had been the special concern of a group of ardent and industrious naturalists. Thereafter it became the driving force of a body of experimental science. Between the modern standpoint and the two great bodies of evolutionary speculation associated specially with the names of Lamarck and Darwin, there is thus a fundamental difference of approach. The ideas of Lamarck, Buffon, Erasmus Darwin, St. Hilaire, Goethe and Robert Chambers first presented the evolutionary problem in definite terms. The contribution of Darwin and Wallace first gained general acceptance for the doctrine of descent. But in the light of modern knowledge the success of these latter cannot be said to have been due to the

greater measure of experimental data on which their conception of the process was based: for, like Lamarckism, Darwinism was an essentially dialectical construction.

Those among Darwin's followers who followed the example of Weismann (1876) in rejecting the Lamarckian doctrine were forced to formulate the theory of Natural Selection in a much more rigid form than had its original authors. The belief that species can be indefinitely improved by

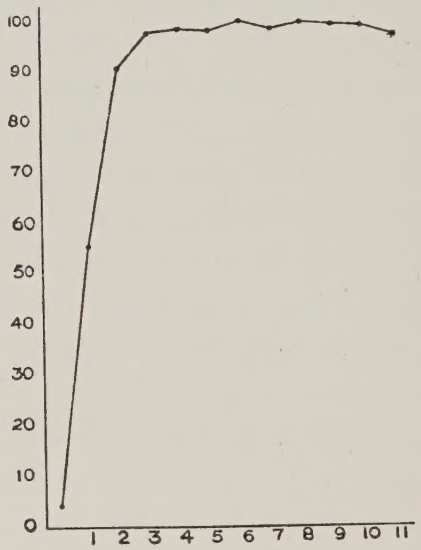

FIG. 125—DIAGRAM ILLUSTRATING THE RESULTS OF SELECTING FOR EXTRA BRISTLES IN DROSOPHILA MELANOGASTER. SELECTION AT FIRST PRODUCES RAPID EFFECTS, WHICH SOON SLOW DOWN AND THEN CEASE

selection alone came to be widely held, until Johannsen's statistical experiments upon beans showed very clearly that selection can only sift out from a mixed population certain individuals with distinctive hereditable properties. Abundant experimental evidence is now available to show that, when a population has been separated into pure-bred types, the breeder's art is at an end. (Fig. 125.) In setting forth the evidences for evolution in a new form Darwin collected, it is true, a large mass of detailed information about domesticated varieties of animals. Whether the fancier

or the stock breeder had merely built up new combinations of hereditable properties that were already present in the stocks with which he dealt, or whether on the other hand new hereditable properties had made their appearance during the process of domestication and selection, he was not in a position to know. If we mate a rose-comb fowl with a pea-comb, we obtain a new combination, the walnut-comb; and the second generation of the cross will consist of walnut, rose-comb, pea-comb and single-comb types. Of the walnuts one-ninth will be genetically pure, and mated *inter se*, individuals of this kind will have only walnut offspring. By going on sufficiently long selecting from a mixed collection of pure and impure walnuts, the fancier will eventually hit upon a pair of pure bred individuals, whose progeny will always be walnut-combed.

But the fancier has not brought anything new into being. In the light of what we now know, it is not necessary for him to go to the trouble of selecting for several generations at random. By crossing back a walnut to a single we can deduce at once whether the former is a pure type or not. The experimental method which Mendel introduced enables us to test very simply whether a given individual is pure for a given character or not. We may not be able to distinguish by its appearance a pure tall variety of the pea from a cross-bred, but on mating the former with a dwarf variety we obtain only tall individuals, whereas on mating the latter with a dwarf variety half the progeny will be dwarf type. We may not be able to distinguish by appearance a pure-bred rose-comb from an individual of the first cross-bred generation in a mating between rose-comb and single comb fowls, but whereas the pure-bred bird when crossed to single gives only rose, the cross-bred rose-comb, when mated to single, gives progeny half of which are rose and half single. Not until there existed a critical test for genetical purity could the phenomenon of genetical variation be regarded as an

experimental fact. It was not necessary to Darwin's argument to define clearly how artificial selection operates. The generation for whom he wrote did not see selection simply as an eliminative process, a blundering hit-and-miss method of achieving a result which can be arrived at by more straightforward means. To them there was something essentially creative in the breeder's art. And this view was based not only on a confused and erroneous body of ideas which were grouped under the term " variation," but also on the tacit assumption that characters can be indefinitely diluted by outcrossing. This assumption will now be examined in its historical setting.

The Persistence of New Genotypes. A second aspect of the problem of genetical variation is the special issue with which the Selection hypothesis of Darwin and Wallace is concerned. It is, however, to Mendel that priority must be given in clearly envisaging the essence of the problem. " Those," wrote Mendel,

> who survey the work done in this department will arrive at the conviction that, among all the numerous experiments made, not one has been carried out to such an extent and in such a way as to make it possible to determine the number of different forms under which the offspring of hybrids appear, or to arrange these forms with certainty according to their separate generations or definitely to ascertain their statistical relations. It requires indeed some courage to undertake a labour of such far-reaching extent. This appears, however, to be the *only right way by which we can finally reach the solution of a question the importance of which cannot be over-estimated in connection with the history of the evolution of organic forms.*

The result of Mendel's method is to show us that new forms, having once arisen, provided they attain sexual maturity and bear offspring, transmit their hereditable properties unchanged; that is to say, the new genotype will sooner or later appear again among the subsequent generations in all its purity.

Before Mendel, investigators in hybridisation had considered the individual as the unit for study; hence arose the belief that hybrids are intermediate between the parents, and this belief in its turn engendered the notion that the crossing of a new type back to the parent stock would involve a dilution of the new character, culminating after a number of generations in swamping it out of existence altogether. Evolutionists of the Darwinian period were therefore under the necessity of bringing forward some entirely external machinery to obviate the supposed effect of this swamping, and account for the persistence of new hereditary properties.

Those who are familiar with the controversies of the latter half of the nineteenth century cannot fail to escape the conviction that the success of the hypothesis of Natural Selection is to a large extent attributable to the fact that it disposed of a difficulty which in the light of modern experimental work no longer proves formidable. Darwin's generation believed in the "swamping" of characters by inter-crossing. The reappearance of the parental properties in all their original purity in the F.2 generation of a cross between pure-bred parents disposes of this belief. Though Darwin in his earlier work did not very explicitly deal with the question, it is clear that latterly he combined the notion of a continuous piling up of "variations" in every generation with the belief that the continuous elimination of the less fit prevented the swamping out of existence of those characters which made the individual more fit, and in each generation accentuated them. This belief that selection both originated and preserved new hereditable properties of organisms subsequently gave the Natural-Selection theory its special theoretical importance. Certainly this was the view of Darwin's contemporaries. Writing in the nineties Bateson remarked :—

The belief that all distinctness is due to Natural Selection,

and the expectation that apart from Natural Selection there would be a general level of confusion, agrees ill with the facts of Variation. We may doubt indeed whether the ideas associated with that flower of speech "*panmixia*" are not as false to the laws of life as the word to the laws of language.

To avoid any doubt a more explicit statement from one of the authors of the Natural Selection Hypothesis is worthy of consideration. Let us refer to the section on swamping in Wallace's *Darwinism.*

> He (Darwin) had always considered that the chief part and, latterly, the whole of the materials with which natural selection works was afforded by individual variations or that amount of ever-fluctuating variability which exists in all organisms and in all their parts. . . .

Wallace then proceeds to quote Romanes as saying that

> if a sufficient number of individuals were thus simultaneously and similarly modified, there need no longer be any danger of the variety becoming *swamped* by inter-crossing.

To this Wallace himself adds :—

> I have already shown that every part of an organism in common species does vary to a very considerable amount in a large number of individuals and in the same locality ; the only point that remains to be discussed is whether any or most of these variations are "beneficial." But every one of these consists, either in increase or diminution of size or power of the organ or faculty that varies. . . . If less size of body would be beneficial, then, as half the variations in size are above and half below the mean or existing standard of the species, there would be ample beneficial variations.

The implication is that natural selection by cutting off the other half—the ample non-beneficial variations—prevents the swamping of the beneficial ones out of existence. We know to-day that this notion of the swamping effects of intercrossing is mistaken. With its dismissal, the *argumentum ad hominem* that made natural selection the

agency for preserving the new hereditary property becomes unnecessary.

Nevertheless it may still be asked what chance a given mutant has of surviving to sexual maturity. This question demands serious consideration, because we know that a very small percentage of animals that are born into the world do actually survive till the age at which reproduction is possible. It has been estimated that if all the offspring of a single female Aphis (the green plant-louse) survived in every generation the total of individuals produced in twelve generations would be 10^{22}. Since a single aphis is about a tenth of an inch long, this number would cover the face of the globe, though twelve generations in the case of the aphis would occupy less than three years.

Evidently the chance of a given mutant form surviving depends on two things: first, whether it possesses any characteristics which favour its survival more than the parent form; second, whether it appears once or many times in the same stock. We now know that the same mutants appear again and again. There seem to be definite *loci of instability* on the chromosomes. Which of these two considerations is more important is not finally settled. Most biologists still incline to regard the former as more significant, though the significance of the second is becoming increasingly realised. Many biologists continue to speak of the selection of mutants by competition for the means of living, as if the recognition of the former were equivalent to Darwin and Wallace's doctrine of Natural Selection; but this can hardly be regarded as justified by the writings of the Selectionists of the nineteenth century. They regarded Selection as not merely the means by which individuals with new hereditable properties are either preserved or eliminated, but the means by which the new hereditable property itself is conserved. Darwin himself, in the *Origin of Species*, was not so explicit on this point as

Wallace in the passage cited. But Darwin does define Natural Selection as a continuous process operating in every generation on differences between offspring and parents of whatsoever origin.

Weismann was even more explicit than Wallace in emphasising the essentially creative rôle of Natural Selection. "The transformation of a species," he wrote,

> as well as the preservation of its constancy are based upon natural selection, and this is incessantly at work, never ceasing for a moment. (*Germ Plasm*, p. 414.)

Weismann was forced to state his view of the Natural Selection hypothesis in this rigid form by the logic of his own position. His challenge to the Lamarckian principle was issued in the period that intervened between the discovery of fertilisation by Hertwig and Fol (1875) and the elucidation of the reduction and maturation of the chromosomes by Van Beneden and Boveri in 1881-3. Later he elaborated a theory of heredity and variation which was based upon the interpretation of reduction generally current until the study of heteromorphic chromosomes by Strasburger, Sutton and others led to the recognition of the segregation of the maternal and paternal members of a pair. It had been generally held before this that the split took place in the reduction division so that each chromosome going to each pole was one half maternal and one half paternal. Thus reduction was interpreted by the early observers to imply not a segregation of maternal and paternal elements but a mingling and dilution that well accorded with the then current conception of what was involved in crossing different types.

As Weismann's views on hereditary transmission in this respect conflict with what we now know to be the facts about chromosome behaviour, there is no need to refer to them in greater detail. They are of interest chiefly as

indicative of the view of natural selection held by Darwin's contemporaries. Darwin himself did not, it is true, express himself very explicity on this issue, but the fact that he called his book *The Origin of Species* taken in conjunction with the controversies that arose out of it leaves very little doubt that, except in as far as he was disposed to invoke the aid of the Lamarckian principle, natural selection was to him not merely an explanation of the Origin of Gaps between Species but the essential condition for evolution to take place at all. In the hands of those of his contemporaries like Wallace, Weismann and Romanes, who rejected the Lamarckian doctrine, this view took on, as we have seen, a perfectly explicit form, which may be defined by saying that in a Darwinian universe in which food, drink and shelter were unlimited in supply, no progressive differentiation of new characters could occur.

Now this is not the view to which experimental study has led us. Given unlimited time, in a Mendelian universe in which natural selection did not operate, everything that we know to-day would be present, and much more besides: evolution would have occurred; but the pageant of life would present to the taxonomist a more continuous appearance and the striking gaps which we now see would be filled not by fossil relics, but living forms. Supposing a single white mutant hare arises in a grey stock, segregation ensures that other white hares pure for the white factor or factors will reappear, and these mated *inter se* will breed true to type. It follows on the assumption (not conclusively proved) that it is advantageous for a hare in temperate climates to be grey and in arctic regions to be white, that there will be far more white hares in the long run in northern countries and grey ones in temperate countries. If there were no competitive struggle at all, there would on the same assumption be grey and white hares in northern and grey and white hares in temperate countries. That is to say, that there would have been

the same amount of evolution: the only difference that Natural Selection makes is to give the picture a more discontinuous aspect.

The Selectionist school did not mean this; they would have formulated the problem in the following terms. Of all hares born to a grey parent some are lighter and others darker, and in a region, where it is advantageous to be lighter, the half that are lighter will have more chance of surviving to maturity, so that in any given generation there will be more lighter than darker parents with the result that in every generation the swamping process will always be on the side of the lighter individuals. Darwin postulated that, if this process went on long enough, a white hare would eventually be produced; that such a race would only be produced in the region where natural selection favoured its survival, and that therefore natural selection was the creative agency, or at least a paramount creative agency in the evolutionary process. Without its aid hares everywhere would remain grey, because in every generation the half that are lighter than their parents would always be balanced by the half that are darker.

Thus to cite yet another instance, illustrative of the sense in which the term Natural Selection was employed before the experimental analysis of variation was undertaken, Romanes, in replying to Owen's objection that "the struggle for existence could only act as a cause of the extinction of species not of their origination," remarks that "any agency without the operation of which a result cannot take place may properly be designated the cause of that result." It may thus fairly be said that Darwin himself specifically defines natural selection as a process operating continuously in every generation on all differences between parents and offspring, and that Darwin's contemporaries interpreted this to mean that without natural selection no new types would emerge. As neither of these views is compatible

with the modern standpoint, it would avoid confusion if the term Natural Selection were dropped by those who mean something entirely different.

The modern view of evolution is that new hereditary characters are preserved in virtue of the behaviour of the chromosomes. In the long run individuals possessing these characters survive or die according to whether they are better or worse equipped in the struggle for existence. In this sense selection accounts for the gaps between species, not for the origin of species.

A recent study by Harrison illustrates the elimination of a genetic type in nature. A little over a century ago a large wood in the Cleveland district (England) was divided into two by a stretch of heath. It originally consisted of pine and birch trees. About thirty years ago one section was replanted with birches, and in the other the pines ousted the birches. A species of moth, Oporabia autumnata, has two varieties found in both, but in the pine wood over ninety-six per cent. are of the dark variety, and in the birch-wood eighty-five per cent. are of the light variety. Feeding the caterpillars on birch and pine leaves does not affect the colour of the moth, the two varieties being distinct genetic types. On the other hand a collection of wings lying in the pine-wood showed that although there were twenty-five to one of the dark variety living there, the majority of moths killed by night birds had been of the light coloured variety.

The Adequacy of Geological Time. The evolutionary theory at first had to face a difficulty that no longer presents itself as a positive objection. Kelvin had calculated the possible period of time during which life can have existed on earth from considerations derived from the rate of cooling of the earth's crust. The calculation of the rate of cooling of the earth which Kelvin propounded was subject to the qualification that no factors at that time undiscovered should enter into the question significantly. As a matter of

fact the discovery of radio-activity disposes of the necessity to place any such restriction as Kelvin was led to deduce on the period of geological time. At present we have no reason for believing that geological time is too short to permit of attributing the faunistic changes of successive geological epochs to the operations of the natural process of genetical variation. Nevertheless the Evolution Theory will not stand side by side with the retrospective hypotheses of astronomy in the hierarchy of scientific generalisations until the conditions and frequency of genetical variation have been correlated with more exact knowledge of the duration and meteorological features of the epochs corresponding to geological strata.

The Origin of Species. Having dealt with these three issues we may now turn to a fourth question which has been thrown into sharper relief by modern work. We have said that the modern theory of Evolution could not emerge until the conception of the relative fixity of species had been defined. It is, therefore, a curious fact that, though Darwin called his great work *The Origin of Species by Natural Selection*, little attempt was made by the Selectionist school[1] to deal specifically with the species as a breeding unit in the Linnæan sense. Why individuals of a certain kind do not successfully interbreed with individuals of another kind is a purely experimental issue, and since artificial selection has never resulted in the production of intersterile varieties, it is evidently an issue to which the natural selection hypothesis is irrelevant. Moreover the anatomical features which distinguish different

[1] Darwin and Wallace referred to a natural tendency to infertility as forms become more sharply differentiated. This way of cutting the Gordian knot was not only vague and speculative, but, in point of fact, incorrect. Experimentally it is possible by appropriate procedure to induce the sperm of a starfish to fertilise an egg of a sea urchin, while the eggs of one species cannot in many cases be fertilised with sperm of closely related species by any known procedure. Again, the anatomical differences between different strains of fowl are relatively colossal compared with those that distinguish two different species of sparrow.

species within the same genus are often devoid of any evident survival value. Bateson has put this matter tersely in the following passage :—

> Sometimes specific difference (anatomical differences between species) is to be seen in a character which we can believe to be important in the struggle, but at least as often it is some little detail that we cannot but regard as trivial which suffices to differentiate the two species. Even when the diagnostic point is of such a nature that we can imagine it to make a serious difference in the economy, we are absolutely at a loss to explain why this feature should be necessary to species A, and unnecessary to species B, its nearest ally. The house sparrow (*Passer domesticus*) is in general structure very like the tree sparrow (*P. montanus*). . . . They differ in small points of colour. . . . The two species, therefore, apart from any difference that we can suppose to be related to respective habits, are characterised by small fixed distinctions in colour-markings, by a striking difference in secondary sexual characters, and by a difference in variability. In all these respects we can form no surmise as to any economic reason why the one species should be differentiated in one way and the other in another way, and I believe it is mere self-deception which suggests the hope that with fuller knowledge reasons of this nature would be discovered.[1]

The differences which prevent members of one breeding unit, *e.g.* the dog, and another, *e.g.* the cat, freely mating with the production of fertile offspring are various and heterogeneous, and may be associated with profound or only very slight structural differences. In some cases the barrier is simply a structural one ; a small difference in the copulatory appendages prevents successful congress. A very good example of an anatomical species barrier is described by Skaife in two South African weevils which infest cowpeas. *Bruchus quadrimaculatus* and *Callosobruchus chinensis* could not be successfully crossed. " Interspecific crossing among the Bruchidæ," says Dr. Skaife, " is prevented by the remarkable differences in the size, shape and structure of the internal sacs of the males." But a single breeding unit, *e.g* the fowl,

[1] *Methods and Scope of Genetics*—Cambridge University Press.

Gallus domesticus, may comprise an extraordinary range of genetic diversity with such picturesque extremes, *e.g.* as the Buff Cochin, Yokohamas and Silkies. The barriers which define the breeding unit roughly fall into two categories : (1) members of two units may very occasionally be induced to mate and then produce fertile offspring ; (2) members of two units may mate but produce sterile offspring, *e.g.* the mule ; (3) members of two units may fail to produce offspring at all. That is to say, the breeding unit is defined by the fact that its members show very low fertility with members of another unit or are themselves completely sterile with reference to members of another unit.

The first of these barriers, low fertility, is one which is readily subjected to experimental study. The inheritance of high and low fecundity has been repeatedly shown to be amenable to Mendelian analysis. Mutants or sports with relatively low fertility with regard to the parent stock may be presumed therefore to arise like any other character which depends on unit factors in the chromosomes. The second constitutes a special case. In the case of the mule it has been shown that the sterility is associated with the failure to form gametes on account of the difference in the size and number of the chromosomes in the two species ; and we actually have experience of mutations in which the chromosome numbers are multiples of the chromosome number of the parent stock (" triploids," " tetraploids," etc.). Two species of the plant genus *Papaver* with different chromosome numbers when crossed produce offspring fertile *inter se*, but sterile with reference to either parent. As to complete sterility an interesting suggestion has been put forward by Crew. If a form that was completely sterile toward the parent stock were to arise in the ordinary course of things, it would necessarily, unless hermaphrodite, die without issue. However, if two forms arise which bear each respectively a factor which, in the

presence of its complement of the alternate mutant, produces a lethal condition, such forms, though incapable of interbreeding, would mate freely with the parent stock and constitute separate breeding units with reference to one another. This interpretation has been put forward by Crew on the basis of extensive investigation, to account for the production of monstrous calves by inbreeding among Dexter cattle.

To sum up, the study of inbreeding, self-sterility among hermaphrodites and fecundity among domestic breeds amply justifies the view that sterility and other physiological barriers to free intercourse are capable of being inherited according to the Mendelian and chromosome hypothesis. There is, therefore, no reason to suppose that the various anatomical and physiological characters which constitute species barriers arise in a different manner from other anatomical or physiological peculiarities. A host of circumstantial evidence points to the conclusion that the barriers which define species in the Linnæan sense follow the Mendelian law—for example, the incidence of disturbances in the sex ratios of species hybrids with reference to the heterozygous sex, which, as Haldane has pointed out, would be expected if sex-linked factors were involved. The evolutionary problem presents itself in new form as our knowledge of the hereditary mechanism develops. The final justification of the evolutionary argument will be achieved when intersterile mutants have been shown to appear under experimental conditions. We shall then be able to say that new types which display not only structural but breeding discontinuity have arisen in the ordinary course of generation. At present it is only possible to say that we have very good reason to believe they can do so. Bateson over-emphasised the difficulty of the species problem when he said :—

> the production of an indubitably sterile hybrid from completely

fertile parents, which have arisen under critical observation from a common origin . . . is the event for which we wait.

As Morgan rightly comments,

the necessity of putting the mutation theory to the test that Bateson calls for seems to me very doubtful, for while this is one of the possible ways in which a mutant might split off at once from the parent type, it is by no means the only way or even, I think, the most probable way in which species have become separated. . . . There is no one problem of infertility of species and no one problem of the sterility of hybrids, but many problems, each due to differences that have arisen in the germinal material. One or more of these differences may affect the mechanism of fertilisation or the process of development, producing some incompatibility.

The mechanism of genetic segregation ensures that a new hereditable property, having arisen, will be transmitted to the offspring uncontaminated, if the individual in which it appears survives to sexual maturity. If in a promiscuous population of several genotypes a mutant appears which is characterised by low fertility, inability to copulate, etc., with reference to other genotypes, any hereditable properties which it possesses will be, so to speak, fenced off, and become de facto anatomical peculiarities of a species in the Linnæan sense. Thus the origin of species in the strict sense of the term is an issue with which the theory of natural selection is not concerned. On the other hand it is an issue for which modern experimental biology has found a partial solution and for which in the near future probably it will find a complete solution.

APPENDIX I

SUGGESTIONS FOR FURTHER READING

Those who wish to continue their reading in biology to gain the requisite background for a clearer understanding of the subject may consult the following sources:

(A) SCIENTIFIC METHOD AND HISTORY—Karl Pearson: *Grammar of Science* (chs. 1–3); Bertrand Russell: *Our Knowledge of the External World* (chs. 1–3); Ostwald: *Natural Philosophy; Aristotle's History of Animals; Singer's Greek Biology and Medicine;* M. Foster: *History of Physiology;* Briffault's *The Making of Humanity.*

(B) EFFECTOR AND RECEPTOR ORGANS—Lovatt Evans: *Recent Advances in Physiology* (ch. 1); Harvey, *Nature of Animal Light;* Gray, *Ciliary Motion;* Maxwell: *Labyrinth and Equilibrium.*

(C) CO-ORDINATION—Fulton: *Muscular Movement;* Loeb: *Tropisms;* Pavlov: *Conditioned Reflexes;* Parker: *The Elementary Nervous System;* Hogben: *Comparative Physiology of Internal Secretion.*

(D) ENERGETICS AND TRANSPORT—Lovatt Evans: *Recent Advances in Physiology;* Parsons: *Fundamentals of Biochemistry;* Bayliss: *Principles of General Physiology;* Loeb's *Proteins and the Theory of Colloidal Behaviour;* Barcroft: *Respiratory Function of the Blood;* Krogh: *Physiology and Anatomy of the Capillaries.*

(E) REPRODUCTION AND DEVELOPMENT—Loeb: *Artificial Parthenogenesis;* Lillie: *Problems of Fertilisation;* Child: *Individuality in Organisms;* Graham Kerr: *Comparative Embryology;* Morgan: *Experimental Embryology;* de Beer: *Experimental Embryology.*

(F) GENETICS—Morgan: *Physical Basis of Heredity;* Crew: *Animal Genetics;* Crew: *The Genetics of Intersexuality;* Goldschmidt: *The Determination of Sex.*

(G) SYSTEMATIC ZOOLOGY—Shipley and MacBride: *Zoology;* Sedgwick: *Text Book* (3 vols.); *The Oxford Treatise* (serial); *The Cambridge Natural History* (serial); Parker and Haswell: *Text Book* (2 vols.), etc.

(H) PALÆONTOLOGY—Swinnerton: *Outlines;* Smith Woodward: *Vertebrate Palaeontology,* etc.

APPENDIX II

SUGGESTIONS FOR A PARALLEL COURSE OF LABORATORY CLASS WORK AND BENCH DEMONSTRATION

Chapter I.

Use of microscope.

Fertilisation of sea urchin.

Rough dissection of the frog to show genital organs. Examination of living cartilage from shoulder girdle, blood (stained) and living ovarian tissue. For latter dissect away in Ringer's solution (see footnote p. 31), all oocytes of microscopic size. The nuclei are beautifully conspicuous. Compare with oocytes from terminal part of egg tubes of cockroach, examining immediately after removal from body.

Demonstrations : (1) Isolated heart beat of frog, showing reversible stoppage with Ca-free Ringer. (2) Colour change in frog. (3) Live human spermatozoa and live spermatozoa of snail.

Chapter II.

Dissection of frog to show musculature ; microscopic examination of web to show pigment cells in pale and dark animal. Using pithed animals, observe effect of mechanical stimulation (pinching) of sciatic nerve and gastrocnemius muscle in situ. Observation of ciliary currents in roof of mouth of frog and gills of blue mussel, using carmine suspension for latter, and minute pieces of tissue paper for former.

Examination of living fibres of gastrocnemius muscle and bladder of frog.

Examination of ciliate parasites from rectum of frog.

Demonstrations : Prepared slides of muscle, skin and glands.

Chapter III.

Dissection of eye muscles and cranial nerves of skate.

Dissection of nervous system of frog.

Demonstrations : (1) Effect of cutting sciatic nerve of either side (p. 49) on reflex withdrawal of foot in pithed frog. (2) Velocity of nervous impulse—sciatic gastrocnemius preparation. (3) Vagus inhibition of heart of dogfish or tortoise (kymographic).

Chapter IV.

Dissection of abdominal viscera of frog and rabbit.

Demonstrations : (1) Digestion of starch and albumen in vitro by saliva and gastric juice. (2) Carbon dioxide production of frog (baryta method). (3) Oxygen consumption of tadpole by Haldane's method or of adult frog. (4) Air sacs of fowl.

Chapter V.

Dissection of vascular system of frog.

Dissection of vascular system of dogfish or skate.

Dissection of vascular system of rabbit.

Demonstrations : (1) Physical experiment to illustrate the resistance of capillaries (Fig. 42). (2) Effect of injection of pituitrine on pale frogs.

Chapter VI.

Preparation of microscopic slides (stained and fixed) of blastoderm of chick—first, second and third day.

Demonstration models of frog, and amphioxus development.

Demonstration slides of mitosis and reduction in grasshopper and Ascaris.

Chapter VII. (See Appendix III.)

Experimental demonstration of Mendelian ratios using coloured marbles to show operation of laws of chance.

Execution of a normal curve of error with any variable character, such as bean weights.

Demonstration preparations of Drosophila mutants (Turtox products).

Chapter VIII.

Museum demonstration of classification of animal kingdom and Linnaeus' system.

Chapter IX.

Examination of Amœba and Paramecium. Life history of Monocystis.

Demonstration slides of Radiolaria, Foraminifera, common fresh water ciliates, etc.

Chapter X.

External anatomy of Astacus, scorpion, Limulus, millipede and centipede.

Dissection of Astacus (or Palinurus) and Periplaneta.

Dissection of Helix.

Microscopic examination of Hydra.

Dissection of earthworm and external anatomy of Nereis and Hirudo.

Examination of whole mounts and transverse sections of Ascaris, Tænia and Distomum.

Examination of slides and mounts of Amphioxus.

Chapter XI.

Skeleton of frog.

Skeleton of pigeon.

Skeleton of rabbit.

Museum demonstrations. Skeleton of dogfish and bony fish. Scales of Ganoid fishes. Skeletons of salamander (rudimentary ribs) and of reptiles. Principal modifications of pentadactyl limb.

Revision Work on Part II.

Field work with class demonstrations on :

(1) Helminthine and protozoan parasites of frog ;
(2) Fauna of temporary and permanent ponds : identification of rotifers, Turbellaria, leeches, fresh-water Crustacea and mites, Ciliates, etc. ;
(3) Fauna of running water : identification of insect larvæ ;
(4) Fauna of rock pools ;
(5) Cryptofauna of stones and bark, myriapods, apterygota, arachnids, isopods, etc.

APPENDIX III

PROBLEMS IN GENETICS

The essential facts of genetics are unsuited for practical demonstration because of the time-factor involved. It is therefore essential, to ensure a sound grasp of the subject, that the student should work through a series of examples, such as the following, based on actual experimental data.

1. Indicate with the aid of diagrams how the following data may be explained :—

   (*a*) A purple eyed mutant of Drosophila crossed to pure wild stock always gives offspring all red-eyed. These mated *inter se* in one experiment gave offspring 107 red-eyed and 38 purple-eyed.

   (*b*) A yellow male mutant of Drosophila crossed to wild stock females always gives grey offspring. A yellow female mutant crossed to a pure bred wild stock male, has offspring, half of which are grey females and half yellow males.

2. Barred plumage is a dominant sex linked character of the Plymouth Rock breed. A black Ancona hen is crossed with a Plymouth Rock cock and the F.1. males are crossed back to the mother, the F.1. females being crossed back to the father. What are the results obtained ? What would be the result of an analogous experiment in which the reciprocal cross was carried out ?

3. A pure-bred barred rose-comb cock is crossed to a black single-comb hen, rose being dominant. Indicate the constitution of the F.1., the F.2. and the progeny of the black-crosses of the F.1. to both parents. Give a diagrammatic representation on the lines of the chromosome hypothesis.

4. In Drosophila a pure-stock wild (grey-bodied) male is crossed to the mutant yellow-bodied female. The progeny when mated *inter se* gave :—

Grey females	...	52	Yellow females...		53
Grey males	...	49	Yellow males	...	48

With another yellow female the results obtained in the F.2. were :—

Grey females	...	199	Yellow males	...	104
Grey males	...	201	Yellow females...		203

Interpret this result and illustrate with diagrams.

5. Construct a diagrammatic solution of the following problem : In Drosophila vermilion eyes are referred to a sex-linked recessive mutant from the red-eyed wild stock. Certain vermilion-eyed females have vermilion-eyed male and female and red-eyed male and female offspring when crossed to wild type. These females have a Y chromosome in addition to the normal XX group. How would you test their offspring in a cross with red-eyed males to detect differences in genetic constitution of outwardly similar individuals ?

6. The F.1. generation of a cross between single and walnut-combed fowls gave the following offspring, when mated *inter se* :—

Walnut ...	...	211	Rose comb	...	71
Pea comb	...	68	Single comb	...	24

Represent by the aid of diagrams the quantitative results you would anticipate from crossing the F.1. birds to pure bred pea-combed and rose-combed individuals.

7. Pure-bred rose and pea-combed fowls when crossed give walnut-combed offspring. These bred *inter se*, produce walnut, pea, rose and single-combed progeny. Interpret these results :—

   (*a*) Rose by walnut give three-eighths of the offspring walnut, three-eighths rose, one-eighth pea, one-eighth single ;

   (*b*) Rose crossed to pea gave 6 walnut and 5 rose chicks ;

   (*c*) Walnut by single, only one egg hatched out. It gave a single-combed chick.

   Deduce the family history of the parents in each case.

8. In fowls there are four types of comb, known as Walnut, Pea, Single and Rose. No other data are given for the solution of the following experimental results. Four different Walnut birds were used in making the crosses.

(*a*) Walnut A crossed to Single gave offspring :—

Walnut	58	Rose	57
Pea	61	Single	62

(*b*) Walnut B crossed to A gave :—

Walnut	101	Rose	35
Pea	32	Single	9

(*c*) Walnut C crossed to B gave :—

Walnut	32	Rose	11

(*d*) Walnut D crossed to A gave :—

Walnut	85	Pea	28

Represent all these crosses diagrammatically and predict the result of crossing C and D to a single combed fowl.

9. The white plumage of Leghorn poultry is dominant to coloured, feathered shanks is dominant to clean, and pea-comb is dominant to single. If a pure-bred white bird with feathered legs and pea-comb is crossed to a coloured, clean, single-comb fowl, what proportion of the white, feathered, pea-comb offspring in the F.2. will transmit these characters to all their offspring when crossed back to the triple recessive ?

10. When rose-comb, feather-leg, white Wyandottes are crossed to single-comb, clean-shanked, black Anconas all the offspring are black, feather-legged and rose-combed. What would you expect to happen if these offspring were crossed with a pure single-comb, clean-shanked, white Wyandotte ?

11. A black, feather-legged bird with single comb was crossed to a white Wyandotte (rose comb and clean shanks) and the offspring which were black, feather-legged and rose-combed, when mated among themselves, produced a generation of which one quarter of the total number had single combs, one quarter clean shanks and one quarter white plumage. What would be the quantitative results you would anticipate from back-crossing the F.1. to either parent, assuming that no linkage enters into the question. Illustrate with diagrams.

12. In a cross between the yellow-bodied mutant and a male of the vermilion-eyed mutant stock of Drosophila the F.2. generation were as follows :—

Yellow females ...	103	Wild type males	36
Wild type females	98	Vermilion-eyed yellow-bodied males ...	33
Vermilion males	66		
Yellow males ...	64		

Explain this result with a diagram : and determine the probable percentage of the following types :—

Wild type male and female ;
Vermilion, yellow male and female ;
Vermilion male and female,

in the F.2. generation of the cross between a wild type female and a vermilion-eyed yellow-bodied male.

13. When the mutant sable, characterised by black body colour, is crossed to a wild stock male (grey) of Drosophila, the following result is found in the first cross-bred generation :

Grey females ...	78	Sable females ...	0
Grey males ...	0	Sable males ...	75

When the mutant " black " is crossed to wild type males all the offspring are grey, and when the mutant " ebony " which like sable and black, is a black-bodied form, is crossed with wild stock males, the offspring again are all grey.

In a cross between ebony and vestigial mutants the F.1. females crossed back to the double recessive (ebony vestigial) gave :—

Ebony	32	Wild type ...	33
Vestigial ...	29	Ebony vestigial	31

In a cross between black and vestigial the female offspring backcrossed to the double recessive (black vestigial) gave :—

Black	31	Wild type ...	7
Vestigial ...	35	Black vestigial ...	6

From these data determine the constitution of a cross between the male offspring of a black × ebony cross and the female offspring of a sable × wild type cross. Give the genotypes only.

14. Use the following data to illustrate the meaning of linkage (with diagram) and the principle of the linear arrangement of the genes :—

(*a*) In a cross between the vestigial and black mutants of the fruit fly Drosophila the F.1. males were all wild type, and crossed back to double recessive females (vestigial black) gave :—

Vestigial grey...	126	Black long ...	130

Females crossed to double recessive males gave :—

Vestigial ...	832	Wild type ...	173
Black	841	Black-vestigial	181

(*b*) In a cross between the vestigial-winged and purple-eyed mutants, the F.1. wild type males crossed back to double recessive females (vestigial purple) gave :—

Vestigial red-eyed ...	145	Long-winged purple-eyed	152

F.1. females back-crossed to double recessive males gave :—

Vestigial ...	672	Wild type ...	96
Purple ...	651	Vestigial purple	84

(*c*) In a cross between the pure-bred wild type and black-bodied mutants with purple eyes, the red-eyed long-winged F.1. males when back-crossed to double recessive females (black purple) gave :—

Black purple ...	324	Wild type ...	341

F.1. females mated to double recessive males gave :—

Black	14	Wild type ...	232
Purple ...	11	Black purple...	244

15. Construct a map of the second chromosome in Drosophila to indicate the linkage relations of the following mutant recessive genes : black (body colour), vestigial (wings), arc (wings), purple (eyes) from these data :—

(*a*) Black arc × wild type

F.1. females crossed back to black arc give :—

Grey straight	1,641	Black straight	1,180
Grey arc	1,251	Black arc	1,532

(*b*) Black long × grey vestigial

F.1. females crossed back to black vestigial give :—

Grey long ...	283	Black long ...	1,418
Grey vestigial ...	1,294	Black vestigial ...	241

(*c*) Purple vestigial × wild type

F.1. females crossed back to purple vestigial give :—

Purple vestigial...	1,195	Grey vestigial ...	151
Grey long ...	1,339	Purple long ...	154

(*d*) Purple × black

F.1. female back-crossed to purple-eyed black-bodied gave :—

Black red ...	353	Black purple ...	16
Grey purple ...	382	Wild type ...	22

(*e*) Purple × arc

F.1. females crossed back to purple arc gave :—

Purple straight ...	807	Purple arc ...	488
Arc red	752	Wild type ...	578

16. In Drosophila, when a black mutant was crossed to a vestigial mutant, the result of crossing the F.1. males to double recessive females (vestigial black) was :—

Black	976	Vestigial ...	975

The result of crossing the F.1. females to double recessive males was :—

Black ...	... 2,011	Wild type ...	442
Vestigial...	... 1,987	Black vestigial ...	438

What would be the result of crossing the F.1. males to F.1 females ?

17. In Drosophila, when a purple-eyed vestigial mutant was crossed to a wild type individual of pure stock, the F.1. females crossed back to purple vestigial males gave a generation :—

Purple-vestigial...	376	Purple	38
Wild type ...	384	Vestigial ...	42

The F.1. males crossed to double recessive females gave offspring half purple-vestigial and half wild type. What would have been the result of crossing the F.1. males and females *inter se ?*

18. Use the following data to illustrate the meaning of linkage and the principle of linear arrangement of the genes :—

(*a*) In a cross between the vestigial-winged and purple-eyed mutants of Drosophila, the F.1. wild type males crossed back to double recessive females gave :—

Vestigial red-eyed ...	72	Long-winged purple-eyed	68

F.1. females back-crossed to double recessive males gave :—

Vestigial ...	672	Wild type ...	96
Purple ...	651	Vestigial-purple	84

(*b*) In a cross between wild type flies and black-bodied mutants with purple eyes :—

F.1. males back-crossed to double recessive females gave :—

Black purple	648	Wild type ...	682

F.1. females back-crossed to double recessive males gave :—

Black ...	28	Wild	464
Purple ...	22	Black purple ...	488

(*c*) In a cross between the vestigial and black mutants of the fruit fly the F.1. males back-crossed to double recessive females gave :—

Vestigial ...	158	Black	164

F.1. females back-crossed to double recessive males gave :—

Vestigial ...	841	Wild	162
Black ...	839	Black-vestigial...	159

Using the same data predict the quantitative results of back-crossing the F.1. females of a cross between wild type and the triple recessive to triple recessive males.

19. In a certain cross between an ebony female and a vestigial male of the fruit fly, the F.1., freely mated among themselves, gave a progeny of individuals characterised as follows :—

Wild type ...	145	Ebony	37
Vestigial ...	47	Ebony-vestigial	11

Investigate the possible ways of explaining this result, and indicate how your conclusions could be put to experimental test. You may assume that the usual records had been kept for purposes of identification of different parents of the flies.

INDEX

Acalephæ, 222, 232, 233
Acephala, 222, 224, 232, 234
Actinozoa, 233, 241
Adrenal body, 104
Alimentary Canal, 74 (ill.), 107, 109, 242, 247
Allantoidians, 230
Allantois, 109
Alternation of Generations, 254
Amniota (see *Allantoidians*)
Amoeba, 201
Amphibia, 183, 185, 187, 219, 260
— Skull of, 270–4
Amphioxus, 251, 256
Amylase, 79
Anallantoidians, 231
Anemones, Sea (see *Actinozoa*)
Anenteræti, 233
Animalia—
Articulata, 222
Mollusca, 222
Radiata, 222, 232
Vertebrata, 221
Annelida, 183, 220, 222, 223, 231, 233, 234, 242–250
Annulata, 231
Anura, 287
Anus, 74
Apodes, 233
Appendages, 208
Arachnida, 219, 220, 222, 231, 262
Archæopteryx, 261, 263 (ill.), 282, 283 (ill.)
Aristotle, 180, 196, 205
Arteries, 87, 89 (ill.), 93, 102 (ill.)
— Aorta, 93, 98
— Brachial, 93
— Carotid, 93, 98
— Cœliaco-mesenteric, 93
— Iliac, 93
— Pulmo-cutaneous, 93
— Pulmonary, 98
— Renal, 93
Arteries, Subclavian, 93, 98
— Systemic, 93
— Truncus arteriosus, 93
Arthropods, 183, 185, 196, 206–219 (ill.), 220, 223, 231, 234, 262
Ascidiacea, 254
Asexual reproduction, 9–11
Asteroidea, 236
Astigmatism, 41
Atomic principle, 135, 136
Atrium, 92, 98
Attraction sphere, 125
Auditory ossicles, 43
Auricles, 92, 98
Aves (see also *Birds*), 183, 185, 187, 219

Bacteria, 10, 200, 203
Balanoglossus, 254
Barnacles, 218 (ill.), 229
Barry, 202
Bastian, 204
Bataillon, 20
Bateson, 148, 255, 293, 301, 309, 311
Batrachians, 230, 231 (see also *Amphibia*)
Bayliss, 101
Beans, Variability of, 173
Bee, 9
Behaviour, 62–67, 159
Bernard, Claude, 90
Berthellot, 77
Bile, 79, 80
Biogenesis, Principle of, 192, 196–204
Birds (see also *Aves*), 100, 156, 221, 230, 260, 261, 281–283 (ill.)
Black, 84

Blood—
Circulation of, 86, 89
Composition of, 87
Corpuscles, 18 (ill.), 202
Regulation of flow of, 94
Body Cavity, 214, 235, 248
Bone, 265
Boveri, 304
Boyle, Robert, 84
Brachiopoda, 222, 234
Brain, 57, 58 (ill.), 62, 108
Bridges, 158
Bronchus, 81
Browne, Sir Thomas, 131, 198
Bryozoa, 232
Buchner, 77
Buff Orpingtons, 134
Buthidæ, 288
Butschli, 126

Calamoichthyes, 268
Cambrian, 264
Capillaries, 86–88, 95
Carbohydrates, 73, 82, 90
Carbon dioxide, 70, 81, 86
Carboniferous, 260, 264, 268, 284
Cartilage, 17–18 (ill.), 265
Castle, 118
Catalysis, 76, 78
Cell Theory, 202, 229
Cellular Structure, 17–19
Central Nervous System (C.N.S.), 52–62 (ill.), 212, 213, 225, 242, 246, 250, 251, 253, 255
Cephalochorda, 251
Cephalopoda, 222, 224, 226, 227, 232, 234
Cestoda, 232, 246
Chalk, 201
Chameleon, 6, 7, 26, 40, 57 (ill.)
Chemical Co-ordination, 101
Chemistry of body, 72
Chitin, 213, 242
Chiton, 223 (ill.)
Chondrichthyes, 265
Chordata, 183, 251
Chromosome, 124–132 (ill.), 137, 147, 310
— Hypothesis, 145–159
— Map, 159–168
Cilia, 10, 34
Ciliary motion, 34–37 (ill.)
— muscles, 40–41
Ciliata, 233
Ciliated epithelium, 22
Circulation—
Annelida, 243
Arthropod, 213
Fish, 99–100
Frog, 89–96 (ill.)
Human, 97 (ill.), 98
Mollusc, 225
Vertebrate, 214
Cirrhopoda, 220, 222, 230
Classification, 181, 206, 220, 242
— of Arthropoda, 217
— of Organisms, 194
— of Vertebrata, 217
Clawed Toad, 7, 24–26
Cloaca, 15, 75
Cochlea, 42, 43 (ill.)
Cockroach, 130, 206–211
Cœlenterata, 183, 232, 233, 234, 236–242
Cole, 258
Colour Response, 6, 7, 22–26, 102
Combs, Types of, 153 (ill.), 170
Comparative Anatomy, 228
— the Outcome of, 255
Conchifera, 221
Conservation of Energy, 68–72
Co-ordination, 47
Cope, 118, 296
Coracoid, 269, 279
Coral, 239
Corallaria, 232
Cornea, 40
Correns, 137
Cotylosaurs, 275, 280–283
Crayfish, 206–210 (ill.)
Cretinism, 115
Crew, 132, 310
Crinoidea, 236
Cross-breeding, 138–176 (ill.)
Crossing-over, 161–162 (ill), 166 (ill.)
Crossopterygii, 268–270
Crustacea, 219, 220, 222, 231, 234, 262
Ctenophora, 241
Cuenot, 148

Cuvier, 192, 220, 221, 223, 224, 228, 229, 259
Cyclostomes, 183, 219, 230
Cynognathus, 277, 280
Cytoplasm, 125

Dalton, 134
Darwin, Ch., 137, 228, 257, 286, 290, 293, 297, 298, 300, 303, 306
Development, 105–132
Devonian, 268
De Vries, 137, 293
Diaphragm, 81
Digestion, 73–81, 84
Dinosaurs, 281–2 (ill.)
Dogfish, 206, 265 (ill.)
Dominant, 140
Drosophila, 128, 130 (ill.), 148, 154, 158, 171, 184, 293
Ductless Glands (see also *Glands*), 100

Ear, 8, 37, 38, 39, 41–44 (ill.), 64
Echinodermata, 183, 222, 232, 233, 234
Echinoidea, 236
Echiuroidea, 244
Edwardes, Milne, 24, 229, 230, 256
Effector Organs, 5, 22, 47, 48
Egg (see also *Segmentation*), 11–16 (ill.), 18–21, 72, 105, 108 (ill.), 109, 148
Einthoven String Galvanometer, 51
Embryo, 91, 99, 101 (ill.), 106 (ill.), 109–113, 128
Energetics, Laws of, 71
Energy, 68–72
Enteropneusta, 254
Entomozoa, 231
Environment, 116
Enzymes, 76, 78
— digestive, 79
Epithelium, 17 (ill.), 19
Erepsin, 79
Eurypterids, 262, 264
Eustachian tube, 42 (ill.)
Evolution, 179, 306, 307
— Historical development, 196–200
Evolution, Hypothesis, 256, 257, 291, 308
— Problem of, 190–191, 204
— Species problem, 181
Excretion, 82, 83
Eye, 8, 37, 39–41 (ill.), 64, 210 (ill.), 211

Factors, Mendelian, 136, 138
Fat, 73, 78, 92
Fertilisation, 12–21 (ill.), 123, 127
— Physical nature of, 19–21
Fibres, 53, 60
Fishes (see also *Pisces*), 221, 231, 270 (ill.)
Flagellum, 18
Flemming, 126
Fly—
Blow, 37
Fruit (see also *Drosophila*), 159, 168
Fœtal membrane, 110 (ill.), 230
Fol, 12, 304
Foraminifera, 201 (ill.)
Fossils, 201, 257, 259, 260, 269, 295
Fowl, 19, 108 (ill.), 109, 110 (ill.), 111, 142, 153 (ill.)
Frog, 6–16 (ill.), 18 (ill.), 22–33 (ill.), 38–45 (ill.), 48, 53, 58 (ill.), 64, 73–76 (ill.), 81 (ill.), 82, 83 (ill.), 89–94 (ill.), 98, 102, 105–109 (ill.), 111–113, 182, 206, 265 (ill.)

Galen, 30, 51
Ganglia, 53, 57–60, 212, 213, 225, 243, 246, 253
Ganoids, 267–270, 272
Gastric juice, 79
Gastropoda, 222, 224, 227, 232, 234
Gene, 121, 149, 169
— lethal, 171
Genes, Interaction of, 171
Genetic type, Elimination of, 307
Genetic Variation, Principle of, 193, 290–312
Genetics, 134
Genital Organs, 16 (ill.)
Genotype, 121

Genotypes, Persistence of New, 300–307
Genus, 182
Geographical Distribution, 285–289
Geological Succession, 260–285, 289
Gerard, 197
Gill, 35, 37 (ill.), 112, 113, 217, 225
— arches, 99, 113
— chambers, 36 (ill.), 217
— clefts, 99, 101 (ill.), 111, 112–113
Gilles, Pean de Saint, 77
Glands, 7, 19, 22, 32–34 (ill.), 62, 76, 79, 80, 96, 100, 103–104, 114, 122, 211, 246
Glisson, 27
Glycogen, 46, 78, 82, 90, 92
Gonads, 14, 122, 243, 248
Goodrich, 120
Gravity, 38, 45
Gullet, 75
Gut, Embryonic, 109

Haeckel, 223, 242
Hæmocyanin, 88, 213
Hæmoglobin, 73, 87, 88, 213
Haldane, J. B. S., 70, 71, 120
Haller, 45
Harrison, 307
Harvey, 87
Heart, 87, 91–94 (ill.), 95, 97 (ill.), 99 (ill.), 111, 214, 215, 225
— Atrium, 92, 98
— Auricles, 92, 98
— Auriculo-ventricular valve, 92
— Sinus venosus, 91, 92
— Ventricles, 92, 98
Helmholtz, 49
Helminthes, 231
Hemichorda, 254
Heredity, 116, 141 (see also *Inheritance*)
Hertwig, 12, 304
Heterozygous, 140
Hexapoda (see *Insecta*)
Hill, Croft, 78
Hirudinea, 244
Holothuroidea, 236
Homo sapiens (see also *Man*), 184
Homozygous, 140
Hormones, 101
Huxley, Julian, 70, 71, 120
Huxley, T. H., 228, 249
Hybrids, 135, 301
Hydra, 236–239 (ill.)
Hydrozoa, 240

Ichthyosaurs, 283
Infusoria, 202, 220, 223, 232
Inheritance, Machinery of, 133
— Problem of, 134
Insecta, 88, 185, 188, 219, 220, 222, 231, 234, 262, 264
Intestines, 75, 90, 101
Invertebrata, 220
Iodine, 115, 116
Iris (pupil), 40
Isopleura, 224, 226

Joblot, 203
Johannsen, 173, 298
Jurassic, 260, 279, 282, 284

Karroo, 260, 276
Kidneys, 83 (ill.), 103
Kölliker, 18
Kowalewsky, 253
Kuhne, 77

Lacteals, 96
Lactic acid, 45, 82
Lamarck, 116, 220, 223, 242, 289, 297
Lamarckian principle, 118, 295–297, 305
Lamellibranchiata (see *Pelecypoda*)
Laplace, 85
Larval form, 226 (ill.), 255
— period, 113
Lavoisier, 70, 84, 85
Leeuwenhoek, 11, 87, 202, 203
Lepidosteus, 272
Leuckhart, 232, 233, 240
Liebig, 84
Limb, 207, 282–283 (ill.)

Limulus, 264
Linkage, 164 (ill.), 169
Linnæus, 180, 181, 182, 190, 192, 196, 200
— System of, 185
Lipase, 79
Liver, 33, 76, 78, 79, 90, 92, 214
Localised reactions, 5
Locust, 209 (ill.)
Loeb, Jacques, 19, 64
Lung, 81 (ill.), 98
— book, 216
Lyell, 259
Lymph, 96

Malacozoaria, 232
Malpighi, 83, 87
Malpighian body, 83
Mammalia, 183, 184, 185, 186, 220, 221, 230, 260, 278 (ill.), 279 (ill.), 280
— Skull of, 275–279
Man, 14 (ill.), 16 (ill.), 18 (ill.), 19, 39, 40, 42 (ill.), 59 (ill.), 75 (ill.), 80, 81 (ill.), 83, 90 (ill.), 97 (ill.), 98, 109–112 (ill.), 184, 280 (ill.)
Matrix, 19
Mayow, John, 84
Meckel's cartilage, 266
Melanophore, 22–26, 103
Mendel, Gregor, 136–148, 289, 297, 300
Mendelism, 135–148, 294, 299, 300, 301, 305, 310, 311
Mesoderm, 109
Metabolism, 77
Metamorphosis, 111, 113
— Sexual, 122
Micro-organisms, 200
Mitosis, 126
Mollusca, 183, 221, 223–228 (ill.), 232, 234
Molluscoidea, 232
Monkeys, 184
Monotremata, 279 (ill.)
Moray, Sir Robert, 199
Morgan, 148, 165, 312
Moschops, 277, 281
Moth, Magpie, 156
Muller, 49, 54, 293
Muscle, 7, 22, 27–28 (ill.), 31, 45, 58, 82, 95, 104, 207, 242
— striped, 26, 28 (ill.)
Muscular Activity, 207
— Machine, 45
— Movement, 26, 27, 30, 31
Mussel, 35, 36 (ill.), 37 (ill.)
Mutants, 148, 149, 162, 293, 303, 310
Myriapoda, 219, 231, 262, 264
Myzostomida, 244

Nakahara, 128
Nasal Passage, 81
Nemathelminthes, 183, 247, 250
Nematodes, 247, 248
Nemertinea, 234, 247
Nephridia, 244, 246, 252
Nerve Fibre, 212, 239
— afferent, 53, 54, 61, 212
— cell body of, 56, 212
— cranial, 61
— efferent, 53, 54, 61, 212
— Vagus, 61, 95
Nervous system, 48, 52, 92
— Impulse, 49–51 (ill.)
Neurones, 53, 64
Non-disjunction, 158
Notochord, 109, 252, 253
Nucleus, 18, 202
— Division of, 125–129 (ill.)

Oesophagus, 75
Oligochæta, 244
Onychophora, 218
Ophiuroidea, 236
Optic nerve, 40
Organisms, Classification of, 194
Ossification, 270, 271
Osteolepis, 270
Osteozoaria, 230
Ovaries, 14, 15, 118, 122, 127
Oviducts, 15
Owen, 229
Oxygen, 45, 70, 81, 82, 86, 88, 94

Palæodictyoptera, 264
Palæontology, 229, 259
Palæophonus, 264
Palæozoic, 262
Pancreas, 33, 76, 79, 101, 102
Pancreatic juice, 101

Paramecium, 10 (ill.), 17, 34, 201
Parasites, 245, 247, 248
Parthenogenesis, 20, 248
Pasteur, 192, 203
Pavlov, 66
Pelecypoda (see also *Acephala*), 224, 226
Pelmatozoa, 233
Penis, 16
Pepsin, 79
Peripatus, 218, 244, 255, 262
Perla, 128
Permian, 260, 274, 277, 281, 283, 284
Phenotype, 122
Phillips, 118
Pigeons, 43, 206
Pigment cells, 22 (see also *Melanophores*)
— Bile, 80
— Respiratory, 88
Pigmentary effector system, 40
Pinna, 42 (ill.)
Pisces (see also *Fishes*), 183, 185, 188, 219
Pituitary gland, 62, 103
Platyhelminthes, 183, 245 (ill.), 246
Platypus, 280
Plesiosaurs, 283
Polar Bodies, 126 (ill.), 127
Polychæta, 243 (ill.), 244
Polyembryony, 123
Polypi, 220, 222, 233
Polypterus, 268
Polyzoa, 229, 249 (ill.)
Porifera, 183, 240, 241
Pouchet, 203
Precoracoid, 269, 279
Priestley, 70, 84, 88
Prochordata, 251
Proteins, 72
Protista, 194, 200, 202, 203
Protoplasm, 201
Protozoa, 201, 202, 203
Pseudopodia, 201
Pterodactyls, 281
Pteropoda, 222, 224, 232
Puberty, 122
Pure Stock, 135, 136, 137, 299

Rabbit, 206
Radiaria, 220, 232
Radiolaria, 201 (ill.)
Rana (see also *Frog*), 182, 183
Ray, John, 196
Reaction, Reversibility of, 77
Reactivity, 4, 26
Receptivity, 4, 6–9
Receptor Organs, 8, 37–45, 47, 48, 210, 212
Recessive, 140
Rectum, 75
Redi, 199
Reduction Division, 126 (ill.), 127
Reflexes, 47, 48, 56 (ill.), 57, 64, 66, 212
Remak, 229
Reproduction, 4, 9–21 (ill.), 105, 196, 239, 246
Reptilia, 100, 183, 219, 221, 230, 260, 274 (ill.), 275, 278 (ill.), 281 (ill.)
Respiration, 20, 21, 81–82 (ill.), 84–85, 215–217
Response, 22
Retina, 40, 41, 212
Rhynchocephalia, 281 (ill.), 283
Richter, 134
Roesel, 201
Romanes, 305
Roots, Dorsal and Ventral, of nerves, 53, 54
Ross, Alexander, 199
Rotatoria, 232
Rotifera, 202, 248, 249 (ill.)

Sacculus, 43
Salamander, 116, 286
Saliva, 80
Sarcodaria, 232
Scaphopoda, 224, 227
Schleiden, 202
Schwann, 202
Sciatic Nerve, 49
Scorpion, 206, 208 (ill.), 288
Scorpionidæ, 288
Scyphozoa, 240
Scytodermata, 233
Secretin, 102
Secretion (see also *Glands*), 32, 213
Segmentation (see also *Egg*), 17, 18, 105, 109
Segregation, 139

Segregation, Genetic, 140
— Principle of, 129, 135, 136, 169, 176
Selection, Natural, 301–307
Selectionist School, 306
Seminal Fluid (see also *Spermatozoa*), 11, 14
Sense Organ, 8
Sex, Determination of, 129–132
Sex-linkage, 155 (ill.), 156
Sexual Reproduction, 9, 11–21, 239
Shrimp, 38, 44, 64
Siebold, von, 202
Silurian, 260, 265
Sipunculoidea, 235, 250
Skaife, 309
Skeleton, 28, 29 (ill.)
— Mammalian, 275
— Vertebrate, 229, 230, 265–285 (ill.)
Skin, 23, 33, 82
Skull, 28, 269–281 (ill.)
Spallanzani, Abbé, 12, 21, 84, 203
Species, 11, 179, 181
— Origin of, 181, 200, 204, 303–305, 308–312
Spermatozoa, 11, 12, 14–16 (ill.), 18
Spinal Cord, 49, 53, 60, 64, 108
Spindle, nuclear, 125
Spiracle, 215
Spleen, 96
Sponges (see *Porifera*)
Spongiaria, 232
Spontaneous Generation, 203
Squamata, 283
Starling, 101
Statocyst, 44 (ill.), 64
Statolith, 43
Stegocephali, 261, 268, 269, 270, 271 (ill.), 273 (ill.)
Stenodictya, 264
Stimulus, Effect of, 7, 8
Stomach, 75, 76, 101
Strasburger, 126
Succession, Principle of, 193, 256–290
Sugar, 73, 78, 90
Sympathetic ganglia, 59, 60, 95
Synapsis, 127
Systematic Biology, conventions of, 182

Tadpole, 107, 113, 115 (ill.)
Teeth, 112, 277
Teleology, 192
Teleostei, 267
Tendon, 28
Testes, 14, 15, 18, 122–127
Therapsid, 269, 277
Thermopile, 20, 45
Theromorphs, 277, 278, 280
Thompson, Vaughan, 229
Thoracic duct, 96
Thyroid Glands, 103 (ill.), 114, 122
Tissues, 18
Toad, 33, 43, 102 (see also *Clawed Toad*)
Trachea, 81, 88, 215
Trematoda, 246
Triassic, 260, 275, 277, 279, 281
Trilobita, 218, 261 (ill.), 262, 264
Trypsin, 79
Tschermak, 137
Tunicata, 232, 234, 250, 251, 253, 254 (ill.)
Turbellaria, 232, 246
Turtle, 38
Tympanum, 42
Type, Principle of Unity of, 192, 205, 221, 224, 241, 255
Types, Origin of New, 293

Unit character, 169
Ureter, 83
Urethra, 84
Urine, 15, 83, 101
Urochorda (see *Tunicata*)
Urodela, 286
Utriculus, 43

Van Beneden, 304
Van Helmont, 199
Variation, 294, 301
Vegetative Reproduction, 239
Veins, 86, 90 (ill.)
— Abdominal, 91
— Epigastric, 91
— Femoral, 91
— Hepatic, 91
— Hepatic portal, 89, 214
— Inferior vena cava, 91
— Jugular, 91, 96
— Musculo-Cutaneous, 91
— Postcaval, 91

Veins, Precaval, 91
— Pulmonary, 92
— Renal portal, 91
— Sinus venosus, 91
— Subclavian, 91
Venous Circulation, 91
Ventricle, 92, 98
Vermes (see also *Worms*), 185, 186, 189, 220, 231, 233
Vertebral Column, 109
Vertebrata, 39, 55, 88, 183, 220, 221, 230, 234, 251, 260, 262, 264, 268, 269
— Allies of, 250
— Skeleton of, 229, 230, 265–285 (ill.)
Vertebrate and Arthropod—
Classification of, 217
Comparison of, 206–219
Vesalius, 27, 51
Vitamins, 80
Von Baer, 119, 193, 229

Wallace, 193, 286, 293, 300, 302, 304
Warburg, 21
Weismann, 295, 304
White Leghorns, 134
Whytt, 52
Willis, 289
Wolff, 119
Worms, Segmented (see *Annelida*)
— Flat (see also *Platyhelminthes*) 245
— Thread (see also *Nemathelminthes*), 247

X-rays, 293
Xenopus (see *Clawed Toad*)

Yolk, 19, 109
— plug, 107, 108
— sac, 109

Zoophytes, 232, 239

Printed in Great Britain by The Crypt House Press Limited
Gloucester and London

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